# BIOENERGETICS OF ROCKY MOUNTAIN BIGHORN SHEEP

*Ovis canadensis canadensis* Shaw

BY

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Bioenergetics of Rocky Mountain bighorn sheep submitted by Randall W. Chappel in partial fulfilment of the requirements for the degree of Master of Science in Wildlife Productivity and Management

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ABSTRACT

Winter bioenergetics of captive Rocky Mountain bighorn sheep were delineated by measuring changes in dry matter intake, body weight and resting and fasting metabolic rate from fall until spring. Voluntary consumption of dry matter decreased by approximately 45% from fall to late winter with maximum intakes occurring in early autumn. Generally, body weights increased to January after which stasis or minor weight losses were expressed. Resting metabolic rate at 10°C tended to be relatively stable over winter. Resting metabolic rate at -10°C was lowest in mid-winter, highest in spring and intermediate in fall; a mean downward adjustment from fall to winter of approximately 12% indicated adaptation to lower ambient temperatures. Fasting metabolic rate at -10°C also showed lowest levels in winter with a mean decrease from fall of approximately 14%.

Metabolic response to a range of temperatures from 10° to -30°C indicated that the lower critical temperature of bighorn sheep in winter coat lies near -30°C in still air. Minimum resting metabolic rates occurred at -10°C. No significant metabolic response occurred to wind speeds up to 7.6 $m.sec^{-1}$ at temperatures above -20°C. However, at -21° to -23°C wind speeds of 4.9 to 5.8 $m.sec^{-1}$ effectively raised metabolic rate.

Mean increment for feeding over fasting metabolic rate was approximately 32%. The mean increment for standing over

lying metabolic rate was 18.5%.

Pooled data from all of the trials allowed construction of an explanatory model utilizing the statistical technique of Multiple classification analysis, predictors describing sex, date nutritional status (fed-fasted), trial or exposure temperature, body weight, adaptation temperature 3 days prior to trial, and mean gross energy intake 2 weeks prior to trial were found to exert the most influence on metabolic rate. Up to 87% of the variation in energy expenditure was explained by these variables.

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# 1. INTRODUCTION

Current knowledge of the Rocky Mountain bighorn sheep (Ovis canadensis canadensis Shaw) contains a conspicuous vacuity in even the most basic information on seasonal energy budgets. However, following patterns established in research on domestic animals, researchers have, in the past two decades, made significant contributions towards understanding the energetic basis of interactions of wild ruminants with their environment (Moen 1968, 1976; Shannon et al. 1975; Silver et al. 1969). These discoveries have, in certain areas with various species, remodelled wildlife management techniques through provision of a sound basis for evaluation of the effects of population and habitat manipulation.

The primary function of the bighorn sheep, like all other organisms, is to perpetuate the species. In order to procreate successfully the animal must seek and obtain sufficient essential nutrients and energy to meet the requirements of maintenance, growth, and reproduction. Therefore, motivation for gross distribution and specific habitat selection and use, and social and ecological behavior may be found to a variable extent in the optimization of energy flow to ensure survival (Moen 1973). Thus, the roots of any study of the animal and its environment are wound into the intricacies of bioenergetics.

The energy budget of an animal provides a common base

to which all functions either spatial or behavioral, can be related. Of particular relevance is the definition of the critical thermal environment (Blaxter 1969; Christopherson et al. in press; Moen 1968, 1975; Webster 1974). Approaches vary from delineation of annual metabolic trends under natural or simulated environmental conditions to dissection of the total energy budget into components under carefully controlled conditions.

As this research represents the first investigation into the bioenergetics of bighorn sheep, its primary objective was to delineate important energetic adaptations and to attempt to define their significance. Physiological parameters examined for over-winter fluctuations were voluntary dry matter intake, body weight, resting metabolic rate at warm and cold temperatures, and fasting metabolic rate.

A secondary goal was to investigate the response of the animals to two important interacting environmental stressors, low temperature and wind, and two activities, feeding and standing. These energy increments when added to the basal seasonal energy expenditures allow formulation of a more complete energy budget for bighorn sheep.

In addition to these goals, this study compares the bioenergetics of bighorn sheep to those of other animals, both wild and domestic. From such analysis, it was hoped that unique adaptations might be discovered which could

contribute to the sound management of the species.

## 2. METHODS AND MATERIALS

### 2.1 The Animals and Training

Six female Rocky Mountain bighorn sheep were obtained from Jasper National Park and were bred by rams from Jasper Park at the University of British Columbia. The ewes and resultant six lambs were transported to The University of Alberta in Edmonton in the fall of 1974. During the course of that winter and the spring and summer of 1975 an experimental group of four animals was selected on the basis of tractability. The final experimental group was composed of two yearling rams (M1 and M2) one yearling ewe (F2) and one adult ewe (F1).

Of all of the indigenous species which have been raised in captivity for experimental purposes, bighorn sheep appear to be the most difficult. Various zoological gardens and game farms have been successful as long as sufficient consideration was given to the natural requirements of the animal for psychological and physiological security. The necessity for escape terrain or some form of refuge from stress is of immense importance. Hebert (1973) and McEwan (1975) have successfully used the bighorn as an experimental subject by minimizing handling and contact stress. Generally, researchers have had limited success with maintaining the bighorn in high contact situations. The stress of handling often precipitates a Pasteurella-

pneumonia syndrome which may be the source of high rates of mortality.

In this experiment, where continual handling and instrumentation of the sheep was necessary, importance was placed on minimizing psychological stress. The advantage of having native experimental animals feel at ease in the presence of the experimenter has been noted by Jacobsen (1973). In my opinion this was a major factor in the success of the study, as it resulted in readings more representative than would otherwise be obtained and enabled completion of the research program with the original group of experimental animals.

In order to facilitate this condition, a very gradual period of habituation was carried out over several months in the spring and early summer of 1975. I presented myself and let the sheep make all approaches. All attempts at handling in the post-familiarization period were made with similar caution. Rapid movements were never made in the animal's presence as they appeared to negate any progress attained to that point. However, when cautious handling was obviated, as in the case of early treatments for pneumonia, the requisite action was carried out as efficiently as possible to reduce stress.

Halter training was undertaken over a two month period. The animals were allowed to become familiar with a typical head halter and then attached to leads. The result was a

group of animals which could be led from stalls to metabolism crates with negligible stress, as was reflected in their stable metabolic rate and normal rectal temperature. Franzmann and Hebert (1971) review the effect of stress on body core temperature.

To train the animals for collection of respiratory gases, each animal was held in the metabolic crate a minimum of ten times for gradually increasing durations before the first measurements were made. ROMPUN (xylazine hydrochloride, 20 mg.ml.$^{-1}$), a central nervous system depressant, was administered intramuscularly at one-sixth recommended dosage for dogs ( 10 mg per animal). During initial training the drug was given 1.5 to 2 hours before first recordings of metabolic rate were made. In tests with domestic sheep, statistically insignificant effects on metabolic rate were observed at even twice the dosage administered to the bighorn sheep. Those minor effects produced dissipated within one hour of injection.

The experimental group was moved to a newly constructed isolated pasture in June, 1975. The pasture, approximately 0.4 hectare, was surrounded by a 2.3 meter paige wire fence and bounded on the west by a mature stand of conifers. The trees provided an effective wind break as well as psychological security. Shelter was available in a three sided shed (open end facing south) in which removeable individual stalls for containment during the monthly trials

were constructed.

The importance of the isolated location was two-fold: 1) it removed the bighorns from continual contact with domestic stock kept on the farm from which possible pathogens could be contracted, and 2) it reduced obvious stressful contact with persons other than the experimenter. Both conditions were considered mandatory for successfully raising bighorn sheep in captivity.

## 2.2 Techniques

### 2.2.1. Experimental

Information was obtained primarily from various measurements of metabolic rate. Additional data were collected on dry matter intake of a pelleted ration (Table 2.1), body weights and in some trials, measurements of temperatures which provided the basis for determination of thermal gradients.

The determination of metabolic rate was made by indirect animal calorimetry "based on the close relationship between heat produced when organic compounds are oxidized and oxygen consumed and carbon dioxide produced" (Young et al. 1975). Information from the analysis of respiratory

TABLE 2.1 PELLETED RATION FED TO ROCKY MOUNTAIN BIGHORN SHEEP: COMPOSITION AND PROXIMATE ANALYSIS

| COMPONENT | % in Ration |
|---|---|
| Alfalfa Meal | 25.5 |
| Barley, coarse ground | 31.0 |
| Wheat Bran | 14.0 |
| Beet Pulp | 13.4 |
| Wet Molasses | 7.0 |
| Soyabean Meal | 8.5 |
| Salt (Trace mineralized and iodized) | 0.5 |
| Vitamin ADE Premix (Pfizer) | 0.1 |
| TOTAL | 100.0 |
| PROXIMATE ANALYSIS | |
| Moisture | 8.88 ± 0.7 |
| Crude Protein (Sample basis) | 16.35 ± 0.8 |
| Crude Fiber (Sample basis) | 13.05 ± 0.9 |
| Calcium (Sample basis) | 1.70 ± 0.3 |
| Phosphorous (Sample basis) | 0.82 ± 0.03 |
| Fat (Ether extract) (Sample basis) | 2.95 ± 0.3 |
| Ash (Sample basis) | 8.05 ± 0.2 |
| Gross Energy ($kcal.g^{-1}$) (Sample basis) | 4.26 ± 0.13 |

gases was converted to a measurement of metabolic rate in kcal.hr$^{-1}$ by the equation of Brouwer (1965) where:

$$MR(kcal.hr^{-1}) = (3.866 * l\ O_2) + (1.200 * l\ CO_2)$$

Fasting metabolic rate (FMR) and resting metabolic rate (RMR), are defined as basal metabolic rate (BMR) plus the energy expenditure for physical activity (e.g. the cost of standing), the former being measured in a post-absorptive state (in this experiment after 72 hours of fasting) and the latter being measured after voluntary food consumption. These two energetic evaluations were made seasonally at constant predetermined temperatures of 10°C (thought to be within the thermoneutral zone of the bighorn sheep) and -10°C (thought to be below the lower critical temperature and representative of the minimum temperature to which the environmental chamber could be lowered).

During certain trials temperature profiles and insulation qualities of the tissues and hair coat were determined from measurements of the body core temperature (deep rectal , Tr), and skin surface (Ts) and hair coat surface temperatures (Thc) taken at four points on the trunk (shoulder, anterior rib cage, anterior abdomen, and hind quarter) and two points on the front and hind leg. Exposure temperature (Ta) also was measured.

The plasticized rectal thermocouples recorded rectal temperature at a depth of 7 centimeters. Thermocouple

junctions were placed on the skin surface after carefully parting the hair, and attached using small wound clips which grasped the base of surrounding coat, not actually penetrating the skin. The coat was replaced, so as to maintain as much of the natural insulation as possible. The technique was devised for this experiment and was thought to be superior to the traditional method of shaving a patch and attaching the thermocouple with tape and foam to simulate coat insulation.

A Barnes Engineering Infra-red Thermometer, which is calibrated to the known temperature of a black body, was used to determine the radiant temperature of the hair coat.

Values in $^{o}C.Mcal^{-1}.m^{-2}.d^{-1}$ were calculated for tissues (It), external (Ie), and total (Itot) insulation according to the following equations from Blaxter (1969) and Webster (1970).

$$It = \frac{Tr - Ts}{HP}$$

$$Ie = \frac{Ts - Ta}{HP-0.3}$$

$$Itot = \frac{Tr - Ta}{HP-0.3}$$

where HP (Heat Production) = Metabolic Rate $(Mcal.d^{-1})/0.09 * Body\ Weight\ (BW)^{0.67}$

Voluntary dry matter intake in grams (DMI) was determined daily. Each morning at 8:00 A.M. the animals were

given a quantity of the pelleted ration which was determined to be above the amount they would consume. The next morning, prior to feeding, weigh-backs of the uneaten material were made and individual intake for the previous 24 hour period determined. Water was available ad libitum.

Body weight was measured on a platform scale prior to each trial. A minimum of three values contributed to each monthly mean.

2.2.2. Statistical Analysis

Tests of significance were made using significance of Pearson's r from SPSS subprogram SCATTERGRAM (Nie et al. 1975) or by Students t-test (Steele and Torrie 1960) for comparison of means utilizing a Hewlett-Packard Model 50 programable calculator. Standard errors were calculated by a Hewlett-Packard library program designed for use with the Model 50 calculator.

In Section 5, metabolic rate in $kcal.d^{-1}$, the dependent variable, and several other variables and co-variables were collated and coded in interval scale form. Functions of the OSIRIS III statistical library enabled dissection of predictor variables into categories, described as classes of the predictor, on the basis of important divisions within the predictor scale.

Explanation of variability in over-winter energy

expenditure measured under a variety of experimental conditions was sought through multivariate analysis of the interrelationship of the dependent variable, metabolic rate, and several predictor or independent variables. Multiple Classification Analysis (MCA) (Andrews et al. 1973), a multivariate technique similar to multiple regression with dummy variables, was chosen to examine the correlation between sets of predictors and the dependent variable in the context of an additive model. Initial selection of likely predictor associations was made on the basis of simple correlation between each independent variable and the dependent variable. One hundred twenty four cases provided the data base.

Several statistics were employed to determine the goodness of fit of individual predictors in association with others of the same set and of the model itself. The value of each predictor variable was assessed on the basis of Eta$^2$ and Beta statistics and the subclass coefficients. The Eta$^2$ coefficient, often referred to as the correlation ratio, denotes the portion of variance in the dependent variable explained solely by that predictor. Beta coefficients express the success of each predictor in explaining variation in the dependent variable in association with, and after adjusting for, the effects of all other predictors. It discloses the strength of a given predictor as a member of a set and is similar to partial regression coefficients derived during multiple regression using dummy variables.

The class or category coefficients were obtained through solution of the "normal" or least squares.

The quality of the total model was determined by the R-squared unadjusted value ( the proportion of variance explained ) and the R squared adjusted value. The latter is an estimate of how much variance the model would explain if applied to another group of cases, for example, the population which was the source of the sample group analyzed.

In addition an F value was computed to determine the significance of the predictability of the model on the basis of the following equation (Andrews et al. 1975):

$$F = \frac{E/C - P)}{Z/(n - C + P - 1)}$$

where E is the explained sum of squares, C is the total number of categories across all predictors, P is the number of predictors Z is the residual sum of squares and n is the number of individuals considered.

The MCA program produces a coefficient for each category of every predictor in the model (the class coefficient). The sum of coefficients of categories which apply to the animal or analysis in question, plus the value of the grand mean (average for all cases) provide a prediction of the dependent variable for a given animal as in:

$$Y = y + a + b + \ldots n$$

where a,b, ....n are vectors of coefficients for a given predictor and y is the model grand mean.

2.3 Equipment

The Metabolism Unit of the Department of Animal Science provided the setting and equipment for this study. The refrigerated environmental control chamber was able to maintain temperatures up to 10°C. The minimum temperature which could be attained and held with the heat load of two bighorn sheep was -16°C and that only for a period of approximately one hour. A constant temperature of -10°C to -12°C could be maintained indefinitely.

In addition, a psychrometrically controlled, hermatically sealed, large animal chamber (Young et al. 1975), was used for determining lower critical temperature. The range of temperature available was 10°C to -30°C. The lowest temperature could be reached within one hour, however temperature was reduced in 10° increments over a period of eight to ten hours during most tests to ensure that thermal equilibrium was maintained.

Within the chambers each animal was contained in a specially designed metabolism crate constructed from reinforced expanded metal to allow free flow of heat. Respiratory gases were collected using sealed hoods similar to those of Webster and Hicks (1968), through which fresh air was drawn and from which expired air was withdrawn at 85

1. minute through 4 centimeter diameter polyurethane tubing.

These gases were pumped into a respiratory pattern analyzer which has been described by Young et al .(1975). The basic components of the apparatus were: a gas collector, the respiratory and hood and pump; gas volume and temperature and pressure monitors; gas analyzers, Beckman Para - magnetic Oxygen analyzer ( Model F3M), and Beckman Infra-red Carbon Dioxide analyzer, ( Model 915A); and a Beckman recorder (Model 1005).

Two thermocouple harnesses, each containing seven thermocouples (one rectal and six body surface), were connected to a 24-point Honeywell Centigrade Temperature Recorder, Electronic 16. Thus, the temperature at each site on two animals could be monitored simultaneously and recorded once every three minutes. At approximately fifteen minute intervals a Barnes Infra-red thermometer was used to measure hair coat surface temperature.

## 2.4 Experimental Regime

When the bighorn sheep were not engaged in trials they were maintained on pasture. For at least the first two weeks of each month from August 1975 to June 1976 they were held in individual stalls in the shed, protected from wind, but subjected to ambient temperatures. After an adjustment period of five to seven days, between 8:00 and 9:30 AM on the day of the trial, two animals, F1 and M1, were weighed,

placed in metabolic crates in the experimental chamber or wind tunnel, and harnessed with temperature sensors.

Chamber temperature was lowered to the desired level and after metabolic rates had stabilized, physiological measurements commenced. The stabilization interval generally lasted between one and two hours.

During the three to four hour trial, alternate 10 minute readings for each animal were recorded. Between each 10 minute period, five minutes was allowed for stabilization of the equipment with the respiratory gases of the next animal. The number of individual periods involved in the determination of mean metabolic rate for a given temperature ranged from three to eight. The animals were most calm during the early recordings, becoming progressively more active and irritated as time passed. Observations of general behavior of the experimental subjects in the crates were recorded and when analysis of data was made, only those periods in which the animals were not visibly excited were included. After the trial the sheep were returned to their stalls and the next day the operation was repeated for the other pair, F2 and M2.

Measurements of resting metabolic rate were conducted at both 10° and -10°C every month from August to June to discover if the animals showed progressive adaptation to the lower temperature as ambient temperatures declined, or if, as was initially thought, -10°C was below their lower

critical temperature regardless of season. In addition, every second month from October until June fasting metabolic rate was examined after the animals had been deprived of food for 72 hours.

Measurements of RMR and FMR were made to clarify the possible existence of seasonal adjustments in metabolism similar to those exhibited by cervids (Silver et al. 1969). FMR trials were included in an attempt to partially filter the effect of prior nutrition. A secondary reason for inclusion FMR measurements was to discover if short-term under nutrition created sufficient metabolic stress to raise the lower critical temperature to -10°C in the event that no elevated response was shown during RMR trials at -10°C. RMR and FMR trials were also to provide baseline data to which could be added increments for several components of a more complete energy budget.

During November several observations were made on the energy cost of standing for F1 and M1. In January and March, the availability of the psychrometrically controlled, hermatically sealed, large animal chamber allowed measurement of the metabolic response to a range of temperature from 10° to -30°C. In February and March the sheep were placed in an out-door wind tunnel and respiratory measurements were made over a range of ambient temperatures (-9° to -23°C) at simulated wind speeds of 0, 4.9, 5.8, and 7.6 m. $sec^{-1}$ with the wind striking the animals from the

rear. The animals were held at each progressively lower temperature (during the former tests) and each progressively higher wind speed for approximately 1.5 hours, or until $O_2$ consumption and $CO_2$ production remained stable for a period of at least 30 minutes.

In April, evaluations were made of the increase in energy expenditure over fasting metabolic rate during the act of eating long alfalfa-brome hay. After three FMR measurement periods of 0.5 hour duration, a container of hay was placed inside each respiratory hood. During eating, gas exchange was monitored for 10 minute periods; after four periods had been recorded for each animal, the remaining hay was removed. Respiratory measurements were continued for three 0.5 hour periods after eating.

Behavioral observations were made at every opportunity regardless of whether the sheep were in stalls in the shed, in metabolism crates under trial, or loose in the pasture. Attention was paid to social interactions amongst the animals, activities of bioenergetic importance (eg. selection of advantageous microhabitat, pasturing, shivering and panting) and indications of psychological stress.

# 3. SEASONAL ENERGETICS

## 3.1 Introduction

Several studies have attempted to delineate physiological traits which would enhance the ecological success of wild ruminants. It has been shown that members of Cervidae exhibit annual variations in energetics that occur independent of food availability and whose main stimulus appears to be modification of photoperiod or temperature associated with change in season (Silver et al. 1969; Thompson et al. 1973). Efforts to discover if Rocky Mountain bighorn sheep showed similar circannual rhythms are described in this section.

The physical and climatic environment of the bighorn sheep has been described by Blood (1967), Cowan (1940), Geist (1971) and others. Wild sheep normally experience mild summers with an abundance of high quality forage and harsh winters, with concurrent restricted nutrient and energy sources. Altitudinal migrations are the most apparent ramification of season; the coming of fall motivates movement from alpine summer pastures to low elevation winter ranges. The significance of this seasonal pattern has been examined by Hebert (1973).

Geist (1971), Shackleton (1973), and Stelfox (1975) have documented the effect of season on social and habitat behavior of the bighorn sheep. The onset of winter triggers

a reduction in frivolous social contact. Whereas in mid-summer even mature rams engage in juvenile-like play, rigid interaction patterns are followed in winter to reduce unnecessary energy expenditure in flighty confrontations (Geist 1971). A drastic reduction in the size of the home range is also associated with winter, with the entire herd congregating primarily on south and south-west facing wind-swept slopes and ridges. Snow cover on these areas is minimal due to local climatic conditions thus reducing the high energy expenditure necessitated by foraging through deep snow. The selective grazing ability of the bighorn, noted by Shannon et al. (1975), allows survival on these restrictive areas, although spring often reveals near complete utilization of available forage.

These examples are indicative of the visible responses elicited by season. However, for bighorn sheep, very little is known about physiological and energetic adaptations and their role in over-winter survival. Seasonal variation in energetics operates at its most basic level with changes in dry matter intake (DMI). Under natural circumstances wild ungulates have been observed to reduce their intake from summer to winter. This has long been thought of as only a function of diminished food availability. However, experiments have revealed winter reductions in intake even under ad libitum feeding regimes ( Holter et al. 1975; Silver et al. 1969).

A general pattern has been established which is characterized by voluntary restriction of DMI from late summer or early fall to late winter or early spring, after which intake is increased to a peak in late spring or summer (Hebert 1973; McEwan 1975; McEwan and Whitehead 1970; Nordan et al. 1970; Wood et al. 1962).

If allowances are made for metabolic response time, variation in body weight can be seen to parallel seasonal cycles of feed intake. Changes in weight of mature or near mature animals occur primarily as a result of fat deposition in summer and its utilization in winter. Wood et al. (1962) have examined the growth of black tailed deer from birth to maturity. Although growth curves vary with species the general pattern is similar. Pre-pubertal animals show a phase of rapid growth from birth to winter followed by stasis or a reduction until early summer when accretion is renewed. In their second winter animals experience stases or weight loss. As their genetic potential for growth is approached, both sexes, but particularily the males, begin to exhibit major weight losses over winter.

Between feed intake and change in body weight lie the intricacies of metabolism. The variety of approaches to elucidation of the characteristcs of a particular species' energy metabolism revolve around delineation of baseline energy expenditures under both standardized conditions and specifically defined environmental or nutritional stresses.

Analysis of such data enables quantitative evaluation of the effect of natural and introduced stressors. Although definition and examination of all logical factors which influence the energetics of a given species would appear futile, considerable information is available on seasonal and temperature specific energy expenditures of members of Cervidae.

Theories of cyclic annual variation in the energetics of wild ruminants received initial substantiation from the research of Silver et al. (1969). The confounding effects of seasonal changes in forage intake were partially filtered by examination of fasting metabolic rate (FMR) in adult white-tailed deer after normal ad libitum intake prior to fasting. Investigation of FMR in a thermoneutral environment throughout all months of the year revealed a summer metabolic rate 1.5 times higher than winter (Silver et al. 1969).

Other authors have supported the existence of similar seasonal cycles in metabolic rate, with lowest levels occurring in mid-winter and highest in summer or fall under a variety of standardized temperature and previous nutritional conditions (Holter et al. 1975; McEwan and Whitehead 1970; Thompson et al. 1973; Weiner 1977).

From these studies it is evident that wild ruminants exhibit consistent seasonal variations in DMI, body weight and fasting and resting metabolism. Heart and respiratory

frequency (Jacobsen 1973), rectal temperature (Franzmann and Hebert 1971), occupational patterns (Ozoga and Gysel 1972), total daily movement activities (Jacobsen 1973; Moen 1973; Stevens 1972) and other physiological and behavioral parameters also oscillate circannually.

The existence of an innate, or biological clock, has been established for a variety of small mammals and birds (Krull 1976). Similar mechanisms may control the seasonal variation observed in the energetic and behavioral responses of wild ruminants . The evolution of endogenous circannual rhythms in response to exogenous climatic and biotic cycles may serve to prepare the animal for effective function in advance of the appearance of an environmental stimulus. Thus seasonal cycles in energetics adapt the animal to an anticipated environment, creating efficiency in energy budgeting.

## 3.2 Results and Discussion

### 3.2.1. Seasonal Variation in Dry Matter Intake

A definite seasonal cycle of voluntary dry matter intake (DMI) was apparent for both sexes, although the magnitude of seasonal variation exhibited by females was less than that by males (Figs. 3.1 and 3.2). Within the experimental period, peak intake was reached in early autumn (October) and minimum intake in winter (February - March).

FIG. 3.1 MEAN MONTHLY DRY MATTER INTAKE ($G.KG^{-0.75}.D^{-1}$) OF ROCKY MOUNTAIN BIGHORN SHEEP: FEMALES

(□=F1, +=F2)

$Y = 54.7293 + 14.3696\ MON - 4.8454\ MON^2 + 0.3568\ MON^3$

(MON = MONTH = SEPTEMBER (1) TO MAY (9))

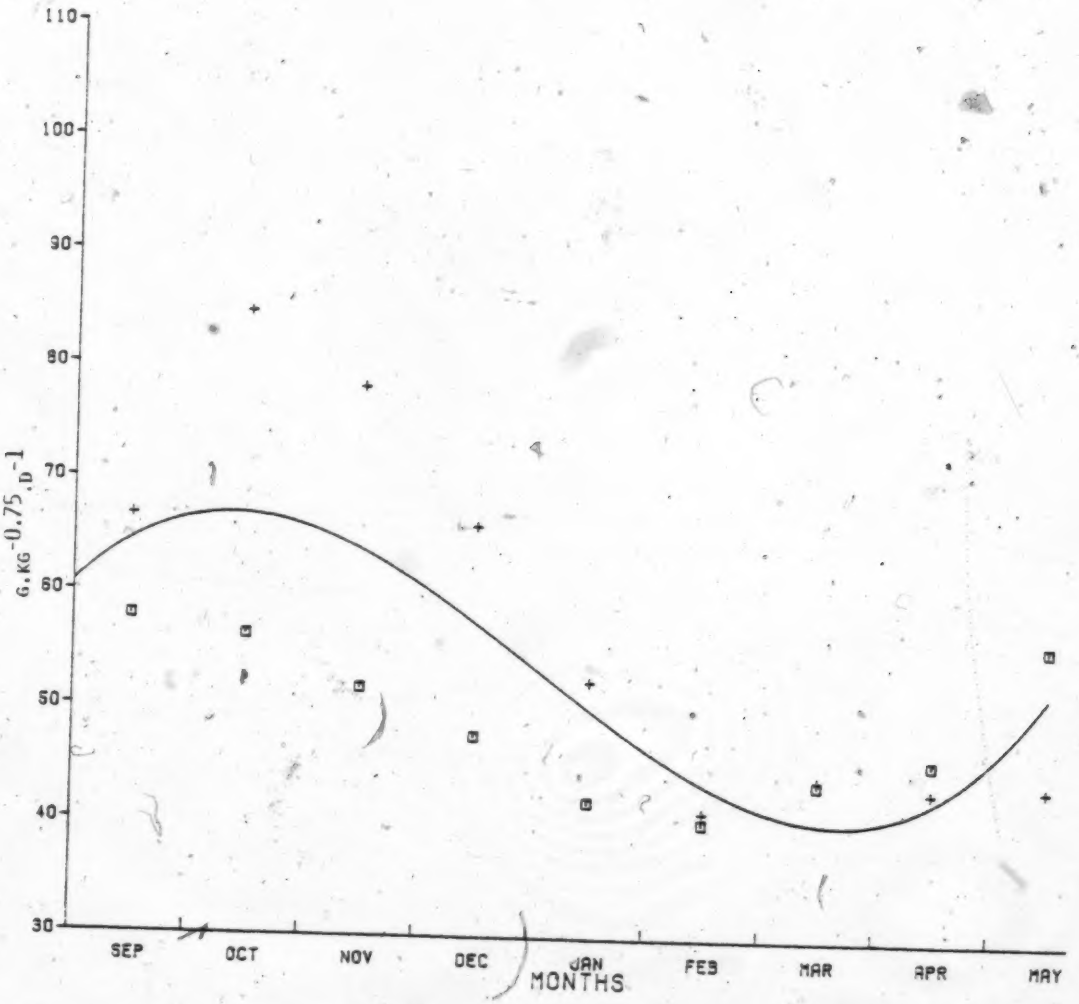
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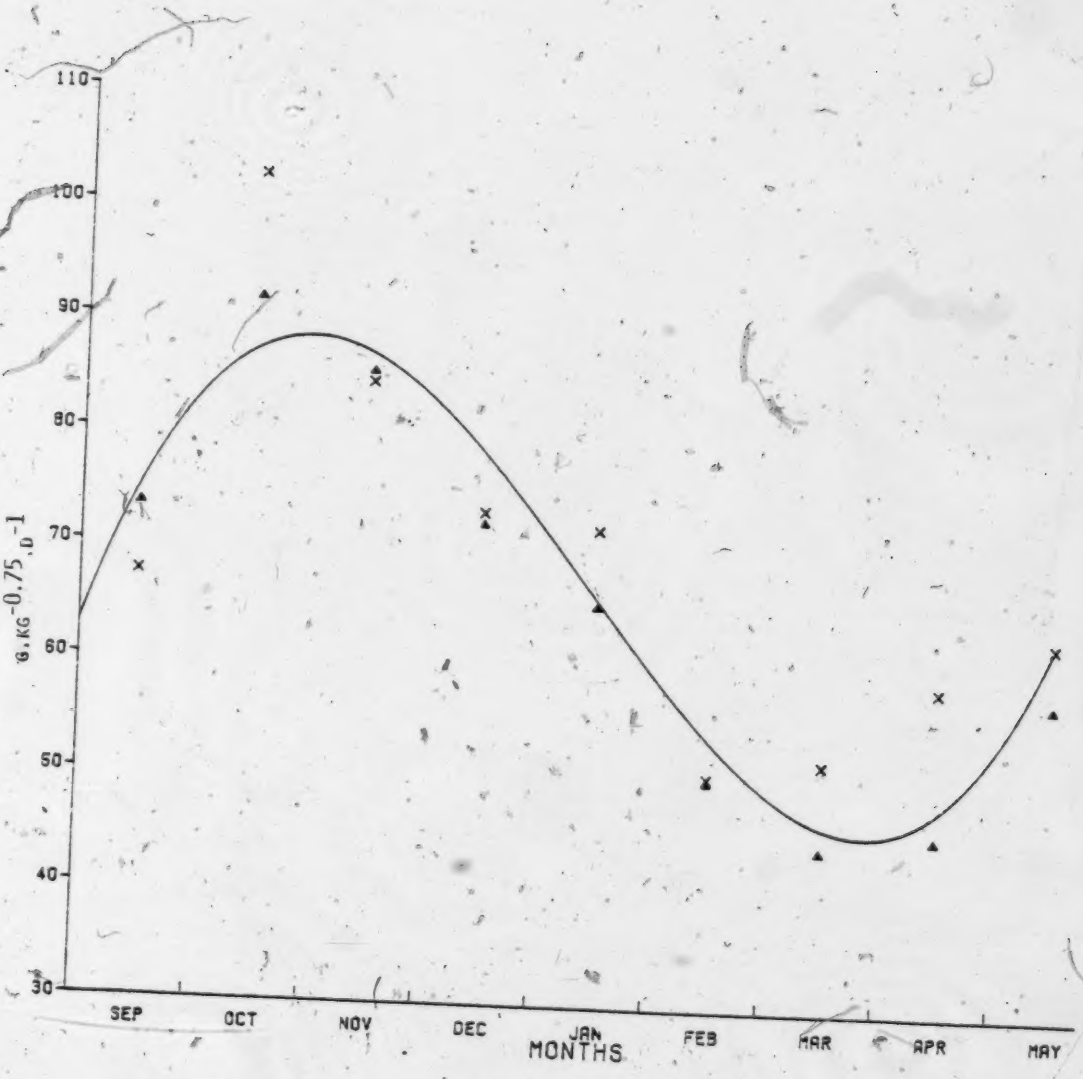
FIG. 3.2 MEAN MONTHLY DRY MATTER INTAKE ($G.KG^{-0.75}.D^{-1}$) OF ROCKY MOUNTAIN BIGHORN SHEEP: MALES

($\Delta$=M1, $\times$=M2)

$Y = 45.918 + 38.9021\ MON - 10.5665\ MON^2 + 0.7169\ MON^3$

(MON AS BEFORE)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Adjustment of mean DMI to $g.W^{-0.75}.d^{-1}$ did not eliminate a significant difference between sexes ($P< 0.01$) or among seasons ($P< 0.005$).

Over-winter decreases in feed consumption of 31 and 52% for F1 (September to February) and F2 (October to February) respectively, provide a mean DMI reduction for ewes of 42%. No significant difference was noted between rams; both reduced intake approximately 52%, although M1 reached his nadir in March, one month later than the other animals.

Increases in DMI to late spring levels from winter lows were 10 and 40% for F2 and F1, respectively, an average of 25%. Rams once again exhibited smaller individual differences with increments of 26 and 30% for M2 and M1. The mean of 28% was not significantly different ($P>0.05$) than that for ewes.

Rams reduced their intake during the rut (late-November to mid-December) by 13 (M2) and 15% (M1) from late October early November levels. These values are in accord with those of McEwan (1975) who noted decreases of approximately 14% in metabolizable energy intake by rams from November to December. The absense of a major increase in feed consumption by F2 in April and May is perplexing and may relate to stress during confinement in her first pregnancy.

### 3.2.2. Seasonal Variation in Body Weight

With the exception of F1 the sheep showed weight gains until January followed by stasis or minor losses until April (Figs. 3.3 and 3.4). The body weight trends exhibited were characterized by less dramatic fluctuations than those common to the cervids (McEwan 1975). Considerable individual differences were evident, particularly between the rams. The rate of gain over winter exhibited by M2 was almost linear. In May his weight at two years old was 87 kg well above the mean weight of four year old rams (Blood et al. 1970). (When three years old M2 weighed 174 kg., over 30 kg more than the heaviest weight reported by Blood et al. 1970)

Maximum weight losses of 8.0% were experienced by F1 and M1; the weight of the ewe fluctuated until February whereas the ram lost weight steadily from January to May. F2 lost approximately 5% of body weight from January to February, then renewed accretion in March. F2 also was above average weight in May; at 66 kg. she was slightly heavier than the mean weight of three year old ewes (Blood et al. 1970).

No significant weight change was associated with the rut. McEwan (1975) noted weight losses of 7 to 16% for breeding rams in general and losses of approximately 8% specific to the age group of the two rams used in this study. Both rams exhibited normal sexual behavior associated with the reproductive season.

FIG. 3.3 MEAN MONTHLY BODY WEIGHT (KG) OF ROCKY MOUNTAIN BIGHORN SHEEP: FEMALES

(SYMBOLS AS BEFORE)

$Y = 55.9286 + 2.8757\ MON - 0.242\ MON^2$

(MON AS BEFORE)

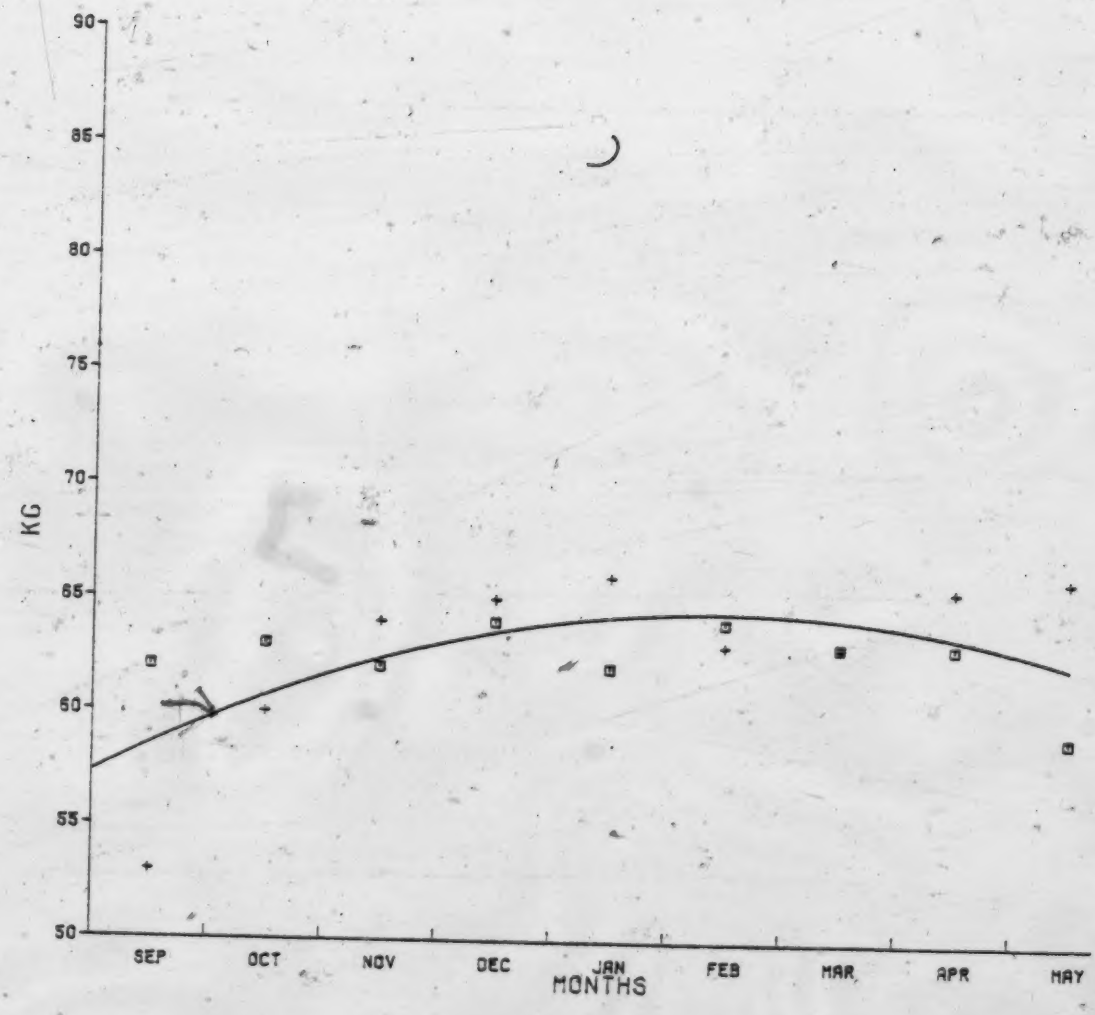
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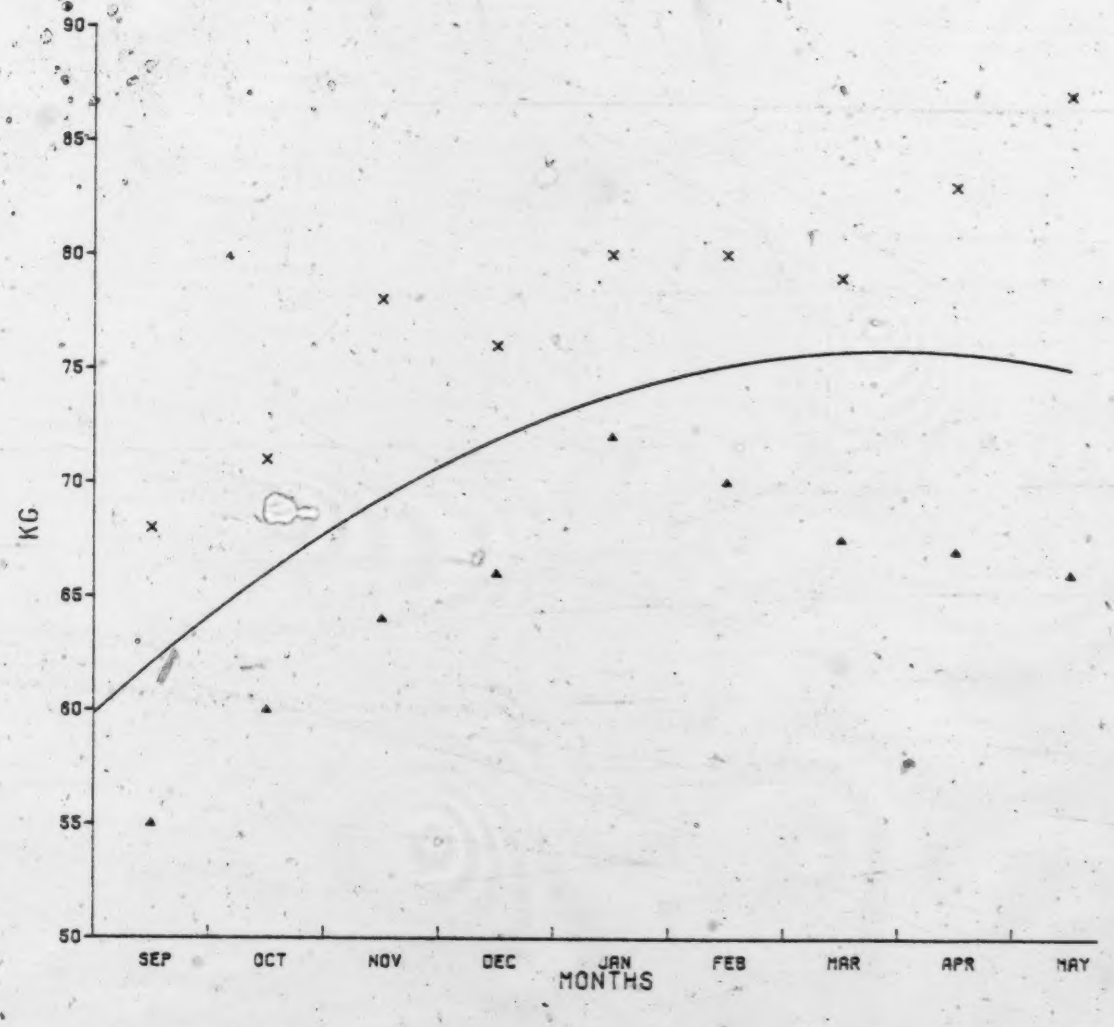
FIG. 3.4 MEAN MONTHLY BODY WEIGHT (KG) OF ROCKY MOUNTAIN BIGHORN SHEEP: MALES

(SYMBOLS AS BEFORE)

$Y = 57.4345 + 4.9554\ MON - 0.3339\ MON^2$

(MON AS BEFORE)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### 3.2.3. Seasonal Variation in Resting Metabolic Rate

#### 3.2.3.1. Seasonal Variation in Resting Metabolic Rate at 10°C

Although significant cycles of metabolic rate ($p<0.05$) at 10° were observed, marked individual differences, particularly between the ewes, made interpretation of data difficult (Figs. 3.5 and 3.6). Differences in energy expenditure between ewes and rams were significant ($P<0.01$).

Generally, a slightly accelerating increase was observed in the resting metabolism of the ewes over-winter, (Fig. 3.5) although individual differences were evident. Averages created by division of the experimental period into fall (September through November), winter (December through February), and spring (March through May) segments provided some clarification. The mean RMR of F1 was 85.9, 90.9, and 111.9 $kcal.kg^{-0.75}.d^{-1}$ during these periods, showing a consistent increase from fall to spring. The means of expenditure by F2 were 103.8, 97.0, and 120.6 $kcal.kg^{-0.75}.d^{-1}$, showing a minor fall to winter reduction. On the basis of these figures both ewes increased RMR from the defined winter to spring periods by approximately 23.5%.

The response of the rams was characterized by smaller individual differences and a slightly stronger effect of season. Delineation of the same three periods disclosed slight reductions in RMR from fall to winter by M1 and M2

FIG. 3.5 MEAN MONTHLY RESTING METABOLIC RATE ($KCAL.KG^{-0.75}.D^{-1}$) OF ROCKY MOUNTAIN BIGHORN SHEEP AT $10^{o}C$: FEMALES

(SYMBOLS AS BEFORE)

$$Y = 89.5533 + 1.0847\ MON + 0.2097\ MON^{2}$$

(MON AS BEFORE)

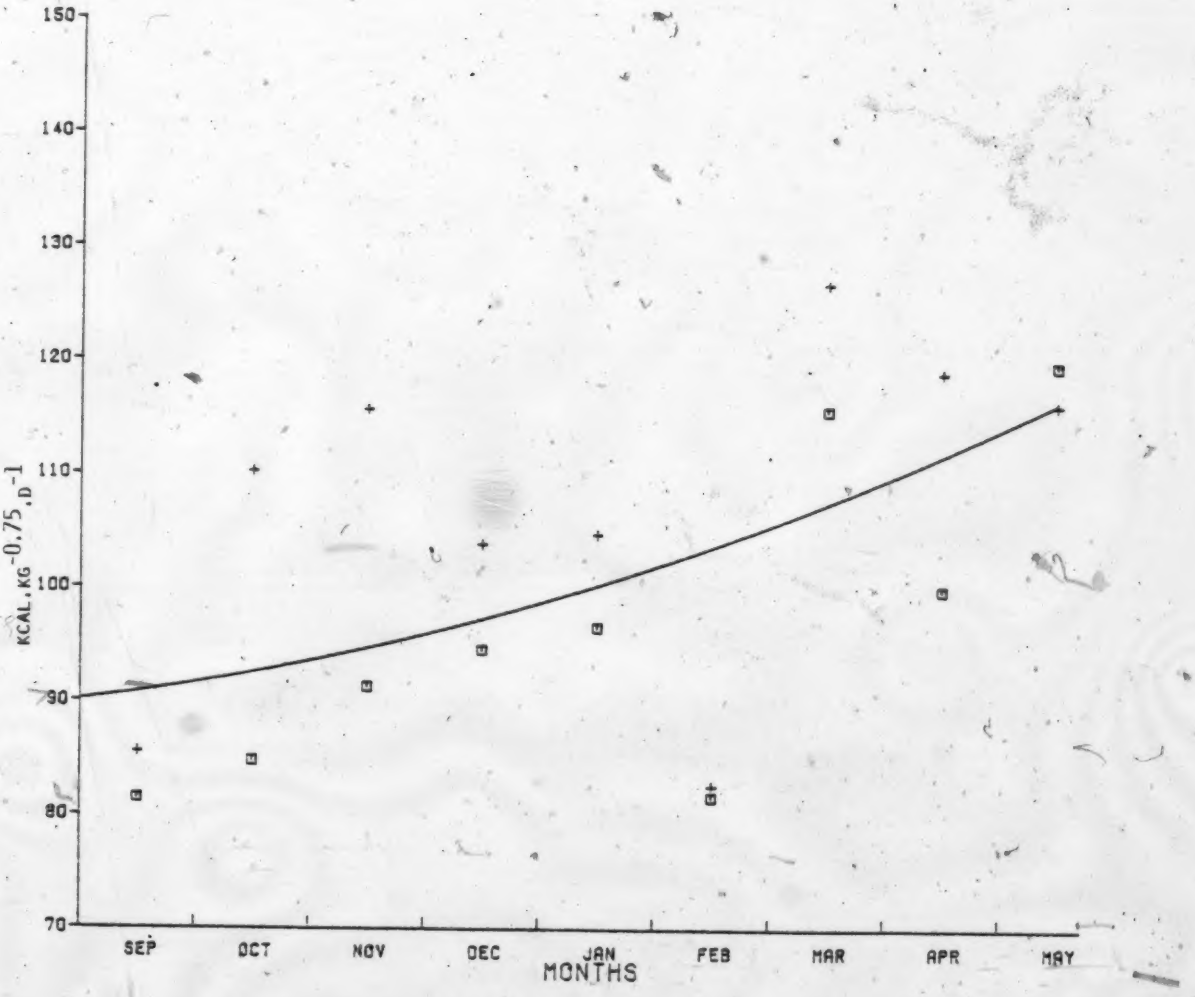
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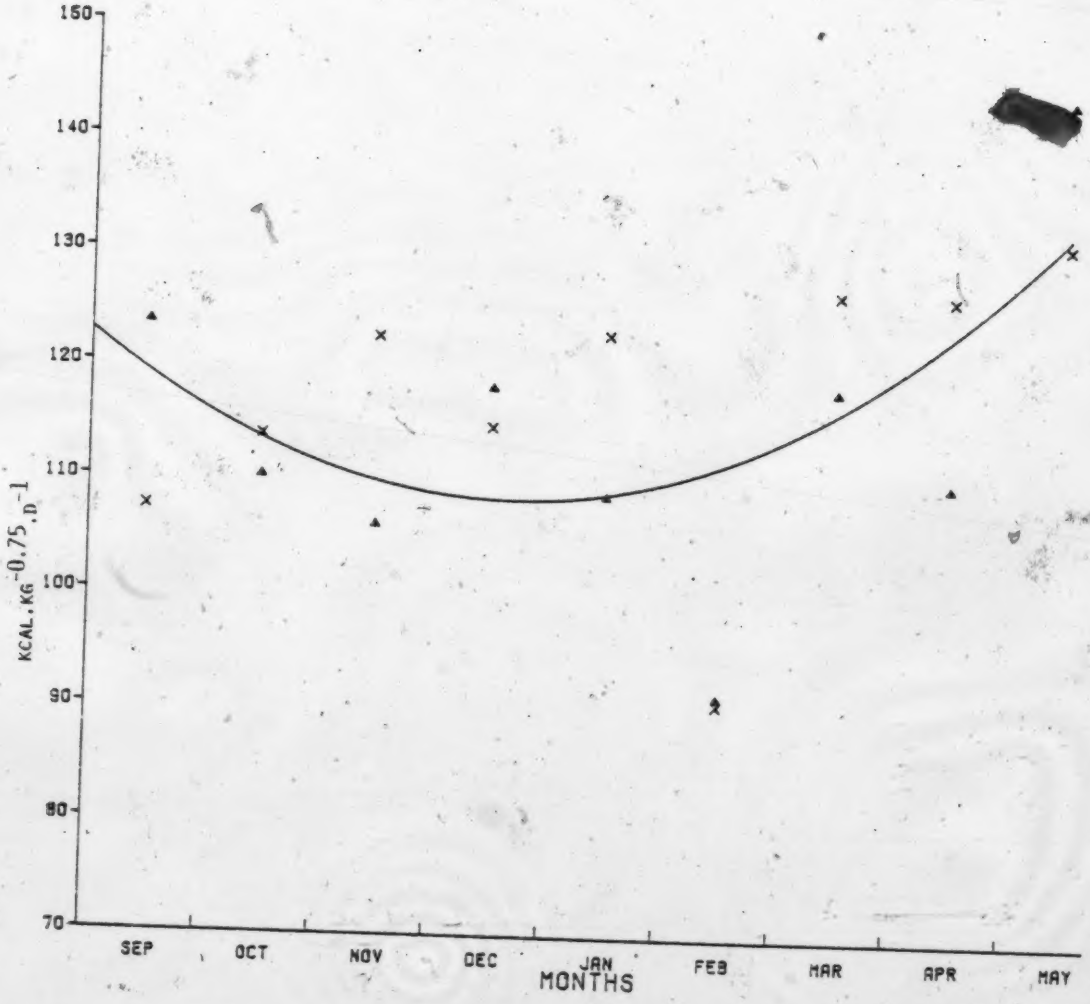
FIG. 3.6 MEAN MONTHLY RESTING METABOLIC RATE ($KCAL.KG^{-0.75}.D^{-1}$) OF ROCKY MOUNTAIN BIGHORN SHEEP AT $10^{o}C$: MALES

(SYMBOLS AS BEFORE)

$Y = 126.8998 - 8.8192\ MON + 1.0457\ MON^{2}$

(MON AS BEFORE)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and an increase of approximately 17% for both animals from winter to spring.

The abnormally low February RMR in both sexes may reflect the influence of unusually high ambient temperatures of 7.5°C, -4.6°C and 0.7°C one day, three days and one week prior to test. It is possible that animals adapted to winter cold stress would adjust their metabolism downward in order to conserve energy during a warm period in winter. The exclusion of February values from the means eliminates any decrease in RMR from fall to winter and reduced changes from winter to spring to approximately 16% for ewes and 10% for rams.

In general, the data reveal little interpretable modification of resting metabolism from fall to winter at 10°C. This suggests that if adaptation or acclimatization to lower winter ambient temperatures occurred, it did not appreciably alter thermoneutral metabolism.

3.2.3.2. Seasonal Variation in Resting Metabolic Rate at -10°C

The seasonal pattern created by resting energy expenditure at -10°C was smoother and more consistent than that at 10°C (Figs. 3.7 and 3.8). Individual deviation from the established trend was considerably reduced. Differences by sex ($P<0.01$) and season ($P<0.005$) were significant.

FIG. 3.7 MEAN MONTHLY RESTING METABOLIC RATE ($KCAL.KG^{-0.75}.D^{-1}$) OF ROCKY MOUNTAIN BIGHORN SHEEP AT $-10^{o}C$: FEMALES

(SYMBOLS AS BEFORE)

$Y = 143.6376 - 20.6803\ MON + 2.0395\ MON^{2}$

(MON = MONTH = OCTOBER (1) TO MAY (8))

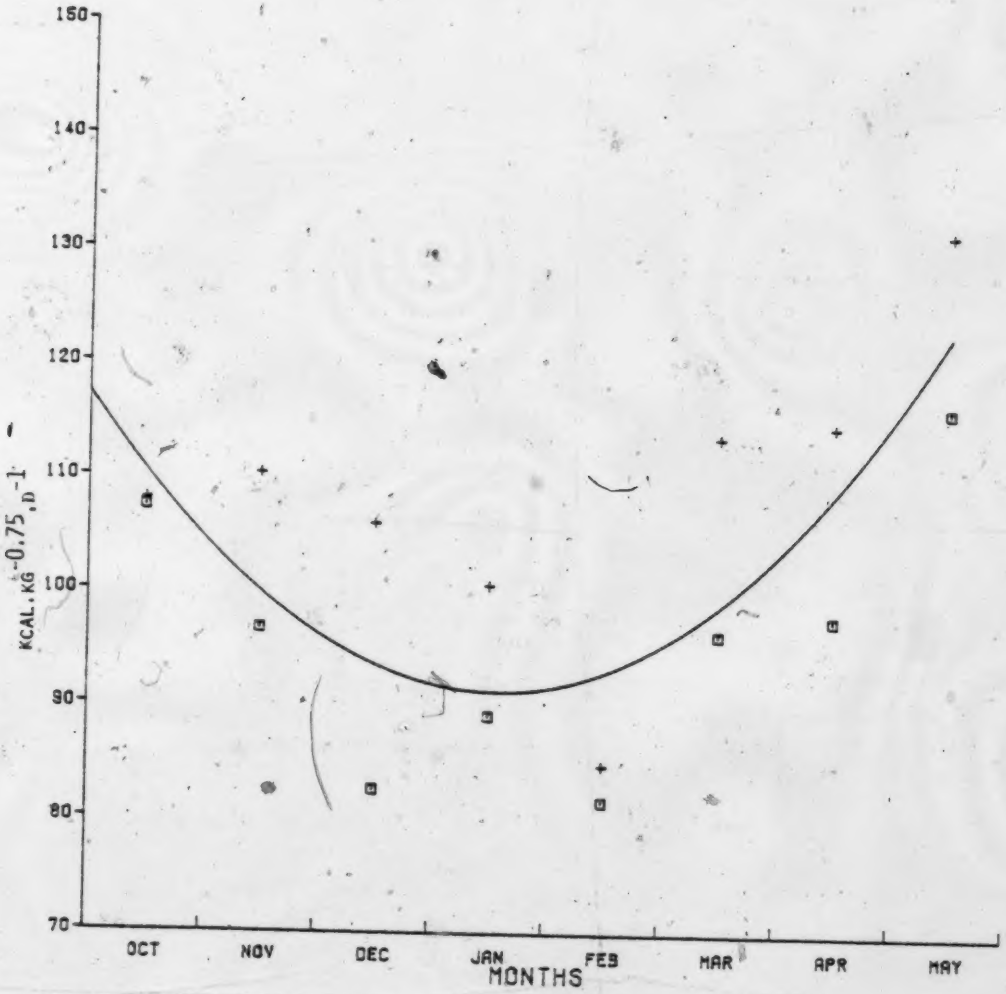
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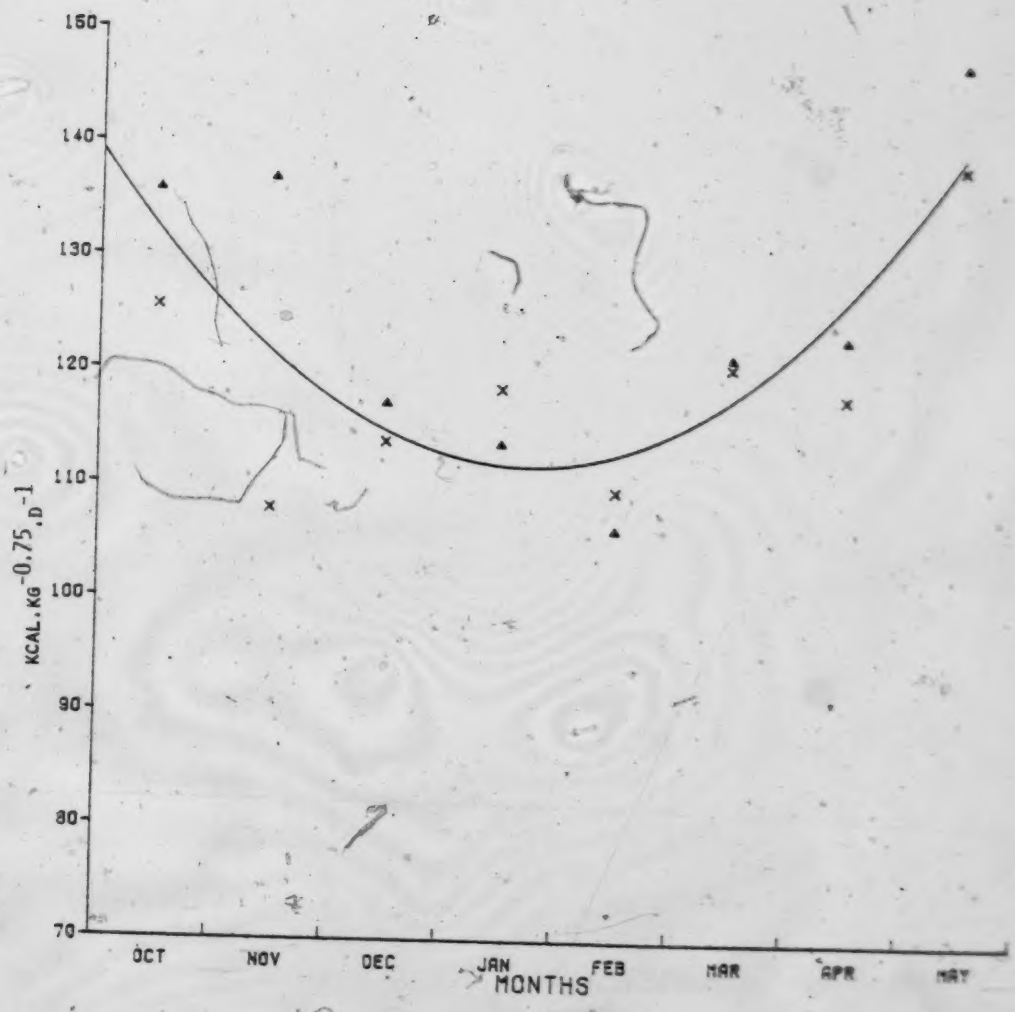
FIG. 3.8 MEAN MONTHLY RESTING METABOLIC RATE ($KCAL.KG^{-0.75}.D^{-1}$) OF ROCKY MOUNTAIN BIGHORN SHEEP AT $-10^{\circ}C$: MALES

(SYMBOLS AS BEFORE)

$Y = 165.5158 - 20.5230\ MON + 1.9545\ MON^2$

(MON AS IN FIG. 3.7)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Division of the experimental period into three seasonal segments created means of RMR for F1 of 102.0, 84.5, and 103.3 $kcal.kg^{-0.75}.d^{-1}$ for fall (October and November), winter and spring (as before). 109.2, 97.1 and 120.0 $kcal.kg^{-0.75}.d^{-1}$ were the corresponding expenditures of F2 during these periods. F1 decreased RMR by 17.2% and F2 by 11.1%. Greater similarity between the animals was evident in mean increases from winter to spring of 22.2% by F1 and 23.6% by F2.

An RMR trend similar to that shown by the ewes was observed in the rams (Fig. 3.8). The seasonal means of M1 revealed a reduction in resting metabolism from fall to winter of 17.6% followed by an increase to spring of 16.2%.

As was the case in trials at 10°C, M2 did not reduce RMR at -10°C as substantially from fall to winter (2.5%) as did M1. His upward adjustment from winter to spring at -10°C was also of smaller magnitude.

In addition, M2 had a consistently lower RMR (with the exception of January) at -10°C than did M1, whereas at 10°C it was generally higher. M2 was always substantially heavier than M1, suggesting the lower RMR at -10°C may be, among other things, a factor of higher volume to surface-area-ratio. Bergmans rule indicates a more favorable heat production to heat loss ratio in cold conditions for larger body sizes. The converse hypothesis would favor greater passive heat loss at higher temperatures for a smaller body

size, explaining M1's lower metabolic rate at 10°C.

No consistent response to the rut was evident in November and December. Only M2 showed an increase in metabolism, of about 5.4%, associated with the hyperactivity of the rut. The other sheep reduced energy expenditures by 4 to 14% from November to December.

A seasonal adjustment in RMR was more apparent in the trials at -10°C than at 10°C. Whereas resting metabolism at the higher temperature revealed little change in response to thermoneutral environments, the pattern of RMR at -10°C indicated progressive reductions occurring from early autumn to late winter. This would appear to be a function of adaptation to decreasing ambient temperature.

### 3.2.4. Seasonal Variation in Fasting Metabolic Rate at -10°C

Cycles in fasting metabolic rate were more strongly developed in rams (Fig. 3.9) than in ewes (Fig. 3.10). However, these figures reveal a prominent reduction in individual differences within sex, indicating the importance of rumen fill and the specific dynamic effect (SDE) of food in determining resting metabolic rate. It was apparent that elimination of feed intake affected the absolute level of energy expenditure, evident in the difference between RMR and FMR, and highlighted the relative importance of adequate nutrition at various times of the year.

FIG. 3.9 MEAN MONTHLY FASTING METABOLIC RATE ($KCAL.KG^{-0.75}.D^{-1}$) OF ROCKY MOUNTAIN BIGHORN SHEEP AT $-10^{o}C$: FEMALES

(SYMBOLS AS BEFORE)

$Y = 119.9562 - 11.2591\ MON + 0.9569\ MON^{2}$

(MON = MONTH = OCTOBER (1), DECEMBER (2), FEBRUARY (3), APRIL (4))

(COMPARATIVE APRIL TRIALS ARE JOINED BY LINES)

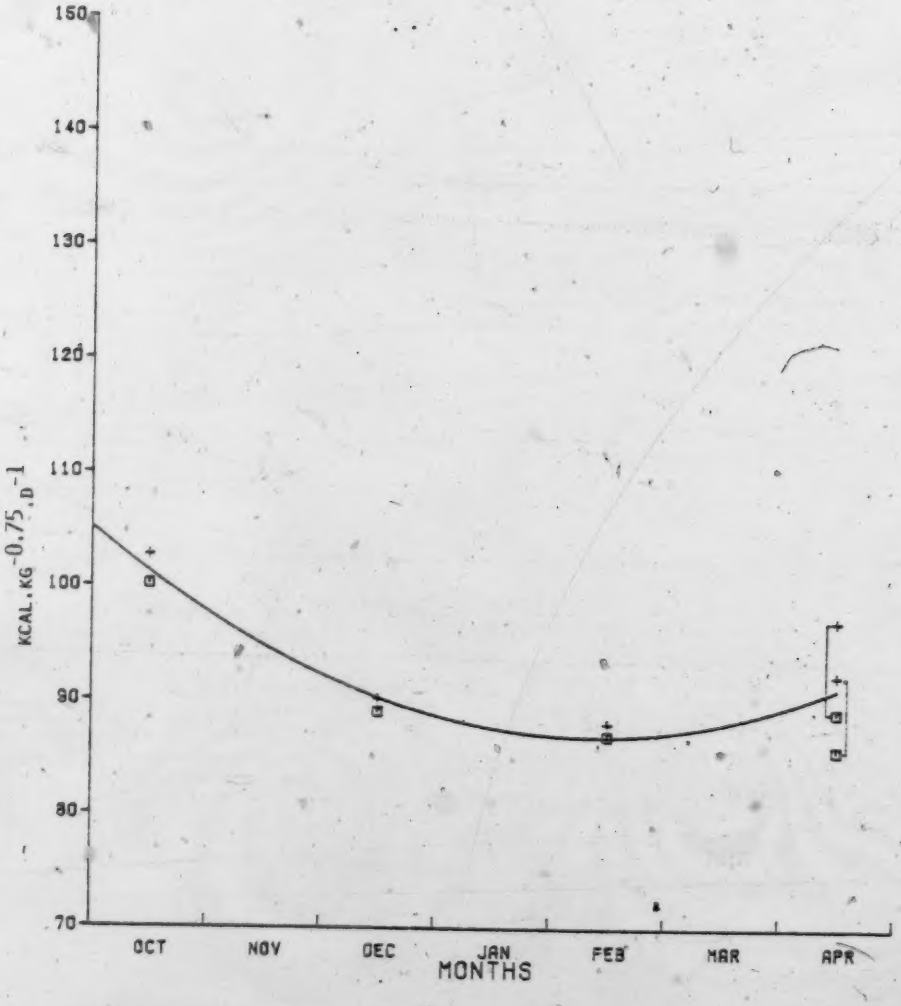
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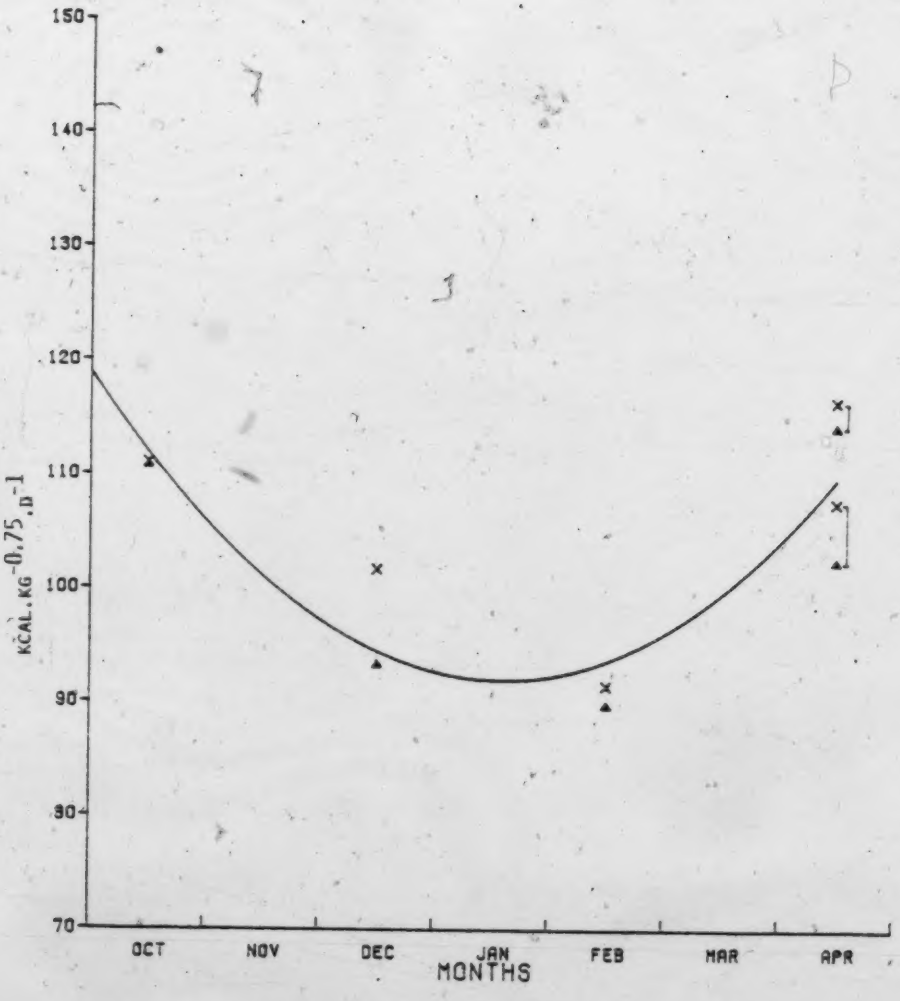
FIG. 3.10 MEAN MONTHLY FASTING METABOLIC RATE ($KCAL.KG^{-0.75}.D^{-1}$) OF ROCKY MOUNTAIN BIGHORN SHEEP AT $-10^{o}C$: MALES

(SYMBOLS AS BEFORE)

$Y = 146.1857 - 21.3122\ MON + 2.0926\ MON^{2}$

(MON AS IN FIG. 3.9)

(COMPARATIVE APRIL TRIALS ARE JOINED BY LINES)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The ewes reduced mean FMR by 12.2% (F1) and 13.3% (F2) from fall to winter. F1 further reduced FMR by 0.5% from winter to spring (mean of April values) while F1 increased her fasting metabolism by 6.5% over winter levels.

M1 decreased FMR by 17.4% from fall to winter and increased 18.4% from winter to spring. M2 showed slightly lower changes with a reduction of 13% from fall to winter and an increase of 15.9% from winter to spring.

Sex differences, as well as individual differences, were smaller than during RMR trials particularly in winter, yet they were still significant ($P<0.05$). The changes in FMR indicated that deprivation of food in spring had a more profound effect on ewes than rams. This phenomenon could be related to pregnancy.

Table 3.2 shows the mean respiratory quotients (R.Q.) of the sheep during fasting trials. At an R.Q. of 0.70 the animal is thought to be receiving most of its energy from the oxidation of fat and thus is truly post-absorptive (Brody, 1945). The bighorns approached 0.70 only during the December trials. This does not coincide with their lowest level of feed intake prior to fasting, but does coincide with the rut. Although their December metabolic rates, as measured in the control chambers, showed no increases in metabolism, sexual activity while in the pasture may have resulted in utilization of most of the energy obtained from feed. This condition appeared to have placed them in a type

TABLE 3.2 MEAN* RESPIRATORY QUOTIENTS OF ROCKY MOUNTAIN BIGHORN SHEEP DURING FMR TRIALS

*Standard error of all values ±0.01

| | F1 | F2 | Ewes | M1 | M2 | Rams |
|---|---|---|---|---|---|---|
| October | 0.76 | 0.78 | 0.77 | 0.78 | 0.79 | 0.79 |
| December | 0.68 | 0.73 | 0.71 | 0.70 | 0.71 | 0.71 |
| February | 0.75 | 0.77 | 0.76 | 0.77 | 0.77 | 0.77 |
| April(1) | 0.77 | 0.78 | 0.78 | 0.75 | 0.76 | 0.76 |
| April(2) | 0.77 | 0.78 | 0.78 | 0.76 | 0.77 | 0.77 |

of elevated maintenance, predisposing them to a more pronounced effect of withdrawal of feed for 72 hours.

The differences in R.Q. between other periods of measurement were not substantial. An average R.Q. of 0.77 was exhibited in October, February, and April trials. Brody (1945) suggests an R.Q. of 0.75 indicates that 15.8% of heat production is from dietary carbohydrates and protein, the rest from body fat. An R.Q. of 0.80 elevates the carbohydrate-protein contribution to roughly 33% of total heat production. Thus it appears that during FMR trials throughout most of the year 15 to 33% of the heat production measured had substrate sources other than fat and much longer periods of fasting should have been employed.

FMR trials indicated greater seasonal changes in the metabolism of rams than ewes. The magnitude of change in FMR from fall through winter revealed a weaker cycle for bighorn sheep than for several species of cervids. In addition, measurements of fasting metabolism during December disclosed a possible strain on the energy budget related to rutting activities that was not discernable in results of other physiological measurements. April FMR pointed to the implementation of a different bioenergetic strategy by rams and pregnant ewes.

## 3.3. General Discussion

Wild northern cervids exhibit a pronounced seasonal

cycle of metabolism characterized by a depression of intake and metabolic rate from fall to winter and a rise from winter through spring (Silver et al. 1969, 1970). This response is evident under a variety of temperature and nutritional regimes. To some degree the results of this research indicate similar trends in the bioenergetics of Rocky Mountain bighorn sheep.

Generally the rams exhibited a more consistent seasonal change in all parameters excluding body weight. Trends in RMR at 10°C from fall to winter were difficult to discern, whereas at -10°C winter metabolism was markedly lower than that of fall or spring. These differences suggest that the animals exhibited an adaptation to the lower ambient temperatures of winter without appreciably modifying their thermoneutral metabolism.

However, the means of adaptation were different than those shown by domestic animals. Webster (1970, et al. 1969) found that sheep and cattle adjusted to the lower temperatures of winter by increasing feed intake and metabolic rate. In contrast the bighorn sheep lowered dry matter consumption and resting and fasting metabolism at lower temperatures.

In April trials the rams appeared to have sufficient body energy reserves to allow a higher rate of expenditure. This may have been due in part to the absence of the energy increment required for pregnency. Support for this theory is

found in a consistent mean decrease in metabolic rate from RMR to FMR of approximately 15.5% in October, December, and February, but a mean decrease of only 8.5% in April.

The ewes, however, demonstrated a much lower and more variable response to fasting. Mean differences in metabolic rate of 5.7 and 4.9% occurred between RMR and FMR in October and December, respectively. In February their mean FMR was actually 5.0% higher than RMR, although this response was complicated by the abnormally low February RMR at both 10° and -10°C. Yet in April 14.1% difference was noted between RMR and FMR. This may indicate the precautionary energy budgeting for late term pregnancy, suggesting conservation of energy which in the wild may mean the difference between a healthy lamb or none at all. It is apparent that ewes and rams have evolved different behavior and metabolism patterns to deal with energy shortages in spring, primarily due to differences in energy requirements.

Examination of body weight by season shows either weight stasis or loss which commenced in December or January and lasted until March. This suggests that energy conservation as revealed in metabolic rate changes did not prevent energy intake from becoming insufficient to meet total energy requirements. To some degree, mobilization of bodily energy reserves was necessitated.

The question arises as to why, given free access to unlimited quantities of the highly palatable ration, these

bighorn sheep did not increase consumption to meet energy requirements. In addition to reducing gross energy intake, the animals decreased metabolic rates, restricted activity while in the pasture, and sought microhabitat within the pen which would reduce energy loss to the environment. These physiological and behavioral modifications would appear adaptive to animals in the wild concerned with conserving energy and thus reducing requirements. However, in consideration of the feed availability for the experimental sheep, the strategy appears non-essential, inefficient, and potentially hazardous to their survival.

The answer to the question posed is largely unknown, but an amalgamation of proven biological effects provides a plausible hypothesis. The basis for this theory is genetic predisposition to circannual variations in metabolism which are triggered by photoperiod changes and controlled by hormonal activity. These metabolic oscillations would adapt the animal to survival in hostile winter environments through anticipation of low temperature and food shortage.

Potential expression of certain physiological and behavioral traits is under genetic control (Saunders 1970;Klopfer 1970). Genetic codes provide the information for specific enzyme production (Saunders 1970) and thus ultimately determine the complete course of metabolism. Although much animal behavior is learned (Geist 1971; Johnsgard 1967) evidence exists that some is inherited

(Klopfer 1970). The rams of this study, although born in captivity and never in the company of mature rams, demonstrated virtually all normal male behavior. Many of the patterns associated with dominance interactions, breeding, and feed selection are extremely complex and no possibility of accidental expression exists.

Sensitivity to photoperiod is also an accepted biological fact, particularly in the lower vertebrates (Ralph 1975) and birds (Krull 1976). Several experiments have been carried out which show that changes in photoperiod are implicated in stimulation of breeding activities and timing of foetal development in domestic sheep (Brody 1945; Yeats 1949) and deer (Moen 1973). Gates (pers. comm.) has shown that bighorn ewes will begin molt and renewed horn growth 1.5 to 2 months earlier than controls, when their photoperiod is artificially accelerated to two times the normal rate of increase from mid-January to mid-March.

Models of control of metabolism are based on a hypothalamic-pituitary-thyroid axis (Di Stefano and Stear, 1968; from Seal et al. 1972). Seal et al. (1972) suggests that the hypothyroidism and reduction of metabolic rate exhibited by deer prior to winter results from decreases in thyrotropin stimulating hormone (TSH) released from the pituitary. The reduction in TSH, they postulate, occurs because of a decrease in thyrotropin releasing factor (TRF) production and release from the hypothalamus. Hoffman and

Robinson (1966) found similarily reduced thyroid activity in white-tailed deer during winter. They also disclosed significantly lower pituitary gland weights.

The mechanism of control of the cycle evident in deer is not understood, however photoperiod has been implicated (French et al. 1970; Hoffman and Robinson 1966; Seal et al. 1972; Silver et al. 1969; Wood et al. 1962). The pathway remains to be established, but the pineal gland, which functions in regulation of seasonal reproductive cycles by inhibition of gonadotropin (Reiter and Fraschine 1969; from Ralph 1975) may be involved. Other indoles or peptides released from the pineal may exert an inhibitory effect upon the pituitary hormone thyrotropin.

Even though the existence of this innate cycle has not been proven beyond doubt, the question remains as to how it could be adaptive to deer and possibly other forms of wildlife. Domestic animals are known to increase thyroxine secretion to augment energy expenditure for meeting the elevated costs of homeostasis during acute or chronic cold exposure (Blaxter 1969). However domestic animals have been bred primarily for productive purposes and several hundred generations of selective breeding have been based on high levels of intake and high rates of gain. These animals counter the effects of winter by elevated metabolism, which they can support given large quantities of feed. Wild animals do not normally have the advantage of unlimited feed

during winter and as a result have adapted to a different bioenergetic strategy for winter survival.

Jacobsen (1973), Moen (1973, 1976), Stevens (1970) and others have established by computer simulation and field experimentation that white-tailed deer exhibit behavioral and physiological traits which result in efficient conservation of energy during winter. Furthermore, Moen (1976) disclosed that under adverse conditions a strategy which involves more time bedded, less time foraging, restriction of movement activities, and careful selection of microhabitat produces the most favorable balance of energy output per unit of energy intake. The indication is apparent that energy conservation favors survival when limited food supply and adverse climatalogical factors prevail.

Geist (1971) notes the existence of a similar conservation response in bighorn sheep. He suggests that they optimize intake over energy expenditure, compensating for increased energy loss by behaviorial and physiological regulation. The bighorns in this study conform to these findings. They reduced metabolic rate in winter, spent more time bedded, less time foraging, and sought out the most favorable environment available to them, selecting bedding sites under conifer canopies or within the shed to reduce radiant and convective heat loss.

The similarity of the seasonal energetics of bighorn sheep to those of the cervids appears to pertain to pattern,

but not magnitude. Comparisons of the metabolic rates of deer and bighorn are difficult, as other researchers often have grouped the findings for different sexes and conditions of being fed or fasted. However, it appears that bighorn sheep exhibit a slightly lower overall metabolic rate during resting trials, compared with white-tailed deer (Holter et al. 1975) and reindeer (McEwan and Whitehead, 1970) and during fasting trials as compared to white-tail deer (Silver et al. 1969).

In addition, the fall-to-winter reduction in resting metabolic rate for both sexes of bighorn sheep was negligable at 10°C, whereas deer reduced RMR by approximately 43% (calculated from Holter et al. 1975, Figure 3). At -10°C, the bighorn sheep reduced RMR by 10.3% as compared to approximately 38% for deer (ibid). Similarly, their mean increase in RMR at 10°C from winter to spring was 20.4% versus approximately 48% for deer (ibid), and RMR at -10°C increased 18.1% as compared to approximately 48% (ibid).

In addition, comparisons of metabolic response at different exposure temperatures indicate that the bighorn sheep, when in full winter coat, have a thermal comfort zone which is lower than that of white-tailed deer in winter coat.

The lower levels apparent in overall resting and fasting metabolism and in adjustment of metabolism by season

are difficult to explore. It may be that the tremendous seasonal changes and generally elevated metabolism shown by the white-tailed deer are characteristics only of cervids. The reindeer examined by McEwen and Whitehead (1970) had higher metabolic rates than the deer. The difference in physiological parameters between cervids and other species examined by McEwan (1975) during the rut supports this hypothesis. The most dramatic reductions in intake and losses of weight were by cervids. Unfortunately, at the time of writing, no reliable metabolic measurements have been made on other wild bovids for comparison.

Secondly, the minimal amplitude of metabolic cycles of bighorn sheep used in this study may be the result of the influence of captivity. However, the absence of substantial difference in metabolic trends between the young ewe F2 and the old ewe F1, who was captured in the Rocky Mountains and merely tamed in captivity, presents some opposition to this theory. In addition, with the exception of the lack of increase in DMI by F2 in spring, their pattern of feed intake is by all available information, typical of animals in the wild (Hebert 1973).

Lastly, the small amplitude of metabolic expression across seasons may indicate that bighorn sheep are very specifically adapted to their selected habitat. In contrast to the wide niche of the deer, the evolution of the Rocky Mountain bighorn has found them successfully adapted to one

very specific ecological niche, and as such they are specialists. The bighorn occupy habitat characterized by more favorable and annually stable micro-climate than that of the general geographical region in which their ranges are found (Geist 1971, Stelfox 1975). They make predictable use of their winter environment (Shannon et al. 1975) reducing energy expenditure over energy gain by selecting less nutritious but more readily available forage and browse of greater species diversity in winter, and conversely, capitalizing on palatable high energy new growth early in spring green-up. There is also a suggestion that sheep take advantage of thermoclines on the slopes and cliffs of their winter range, thereby reducing heat loss by increasing their immediate ambient temperature.

The results of this section of the study indicate that the sheep achieved a mean energy saving of 11 to 14% through reduction of resting energy expenditure during winter. However, consideration must be given to increments over RMR, for example energy expenditure associated with activities such as walking, running, and foraging, and increased heat losses at lower temperatures and in wind. During a season when both quality and availability of food sources can be significantly reduced for extended periods of time, it would seem that the mean energy saving shown would represent a significantly adaptive survival strategy only if combined with other modes of energy conservation such as micro-habitat selection and selective grazing.

# 4. COMPONENTS OF THE ENERGY BUDGET

## 4.1. Introduction

Basal metabolic rate has been used as a starting point for calculating the energy requirements of an animal. However, accurate determinations require extended periods of complete muscular relaxation, a condition which has been found difficult to meet with various wild species. Thus FMR determinations have been adopted as a basic measure of the costs of life functions with partial elimination of the influence of previous dietary effects achieved through fasting, but with inclusion of the energy increment associated with standing. Interspecies comparisons of wildlife must be made on the bases of FMR when possible, and RMR when sufficiently detailed information is not available on fasting metabolism.

Standard measures, for example RMR and FMR, can be used to delineate possible bioenergetic adaptations of a species to its environment. This was the primary objective of the measurements in the first section of this study.

In addition, the RMR and FMR measurements were to provide a baseline to which could be added various increments specific to defined environmental stressors and activities. Dissection of the total energy budget into discrete measureable components enables their combination with a basic cost of maintenance to produce an estimate of

total energy expenditure a procedure standard to the domestic animal sciences.

Energy increments of standing over lying in sheep have been examined by Webster and Volks (1966) and Graham (1964), and by Hall and Brody (1933) for cattle. Expenditures for walking were defined for sheep and cattle by Clapperton (1961) and Hall and Brody (1934) ,respectively. Young (1966), Corbett et al. (1971) and Graham (1964) documented energy costs associated with grazing and eating. Increments due to temperature were described by Blaxter (1962) and Young and Christopherson (1974) and Blaxter (1962) for sheep and cattle, respectively. Wind effects on sheep have been examined by Joyce and Blaxter (1966) and by Webster (1968, 1970) for cattle. Syntheses of components of energy budgets have been made by Blaxter (1969) and others.

Comparable studies on wild species are recent; the difficulty encountered in raising and training wild ruminants has frustrated research efforts. Hammel (1962; from Moen 1973). determined the energy expenditure of a reindeer at rest and while walking with graded work loads. Mattfeld (1973) used the Douglas bag procedure to determine the energy cost of standing, and walking and running through different snow depths for white-tailed deer. Stevens (1972) calculated energy expenditure of deer exposed to wind by computer simulation based on the physical principles of heat exchange. Hart et al.(1961) measured metabolic rates in

caribou with various wind speeds and ambient temperatures. Gates and Hudson (in review) at this laboratory have determined the energy cost to elk of standing and walking at various speeds.

Moen (1968, 1973) utilizes both available information on wildlife and increments for domestic animals to predict energy expenditure. He simulated and tested survival strategies in the wild by examining the combined influence of variable body size, nutritional status, activity increments, microhabitat selection, and environmental stresses on the critical thermal environment. It appears that subtle modification of components of the energy budget, particularly levels of activity and microhabitat selection, can greatly alter total energy expenditure by creating a favorable thermal environment even at temperatures thought to be below the lower critical level.

This approach appears valuable in understanding the functions of the animal within its environment. In this section, attention is given to several important elements which influence the energy budget of bighorn sheep under natural circumstances.

## 4.2. Results and Discussion

### 4.2.1. Metabolic Response Over a Range of Temperatures.

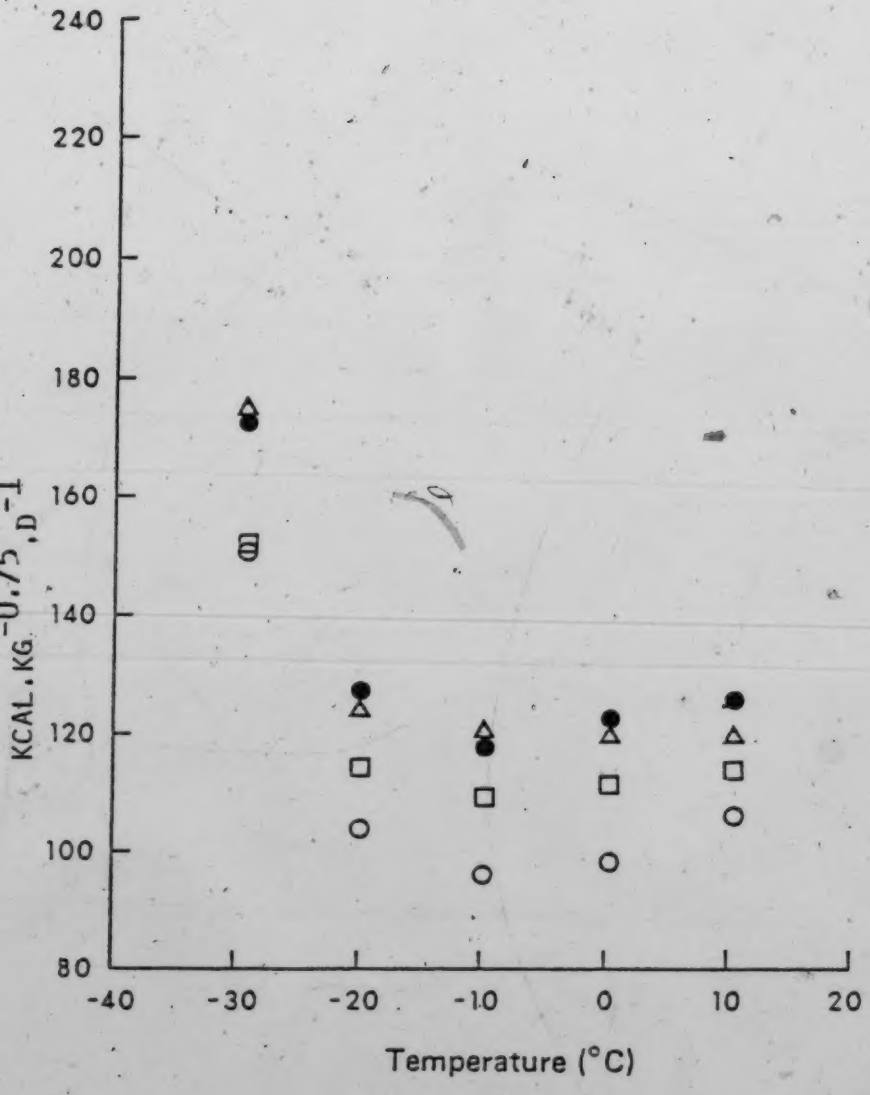
Metabolic rates were almost constant when measured at

temperatures from 10° to -20°C, but increased sharply between -20° and -30°C (Fig. 4.1). Within sex, only metabolic rate at -30°C was significantly different from the response at other temperatures ($P<0.05$). However, significant differences ($P<0.05$) in metabolic rates between sexes were observed at temperatures from 10° to -20°C. All animals had their lowest RMR at -10°C. Mean increments of 39.0% (42.6 $kcal.kg^{-0.75}.d^{-1}$) and 36.9% (46.6 $kcal.kg^{-0.75}.d^{-1}$) were exhibited by ewes and rams, respectively, as temperature was lowered from -20° to -30°C.

The lower critical temperature of bighorn sheep appeared to be near and probably slightly above -30°C in still air. Figure 4.1 indicates only that the rise in metabolic rate occurred somewhere between -20°C and -30°C. However, the recordings made during the trials show that no major increase occurred until chamber temperature neared -30°C.

Virtually all sex differences at -20°C and -30°C were eliminated when based on body weight ($W.^{1}$), rather than metabolic weight ($W.^{0.75}$). Mean increase in metabolic rate was 15.6 $kcal.kg^{-1}.d^{-1}$. Expressed as an increment per degree Centigrade drop in temperature between -20° and -30°C this becomes 1.56 $kcal.kg^{-1}.d^{-1}\ °C.^{-1}$. The changes per degree cannot be treated as more than an approximation since nominal chamber temperatures covered a range of several degrees. For example, metabolic rates at -20° are really a

FIG. 4.1 METABOLIC RATE ($KCAL.KG^{-0.75}.D^{-1}$) OF ROCKY MOUNTAIN BIGHORN SHEEP IN RELATION TO AMBIENT TEMPERATURE IN STILL AIR
(□=F1, ○=F2, △=M1, ●=M2)


240
220
200
180
160
140
120
100
80
KCAL . KG.$^{-0,75}$ ,D$^{-1}$
-40
-30
-20
-10
0
10
20
Temperature (°C)

composite of many measurements made between -19° and -21°C.

The lower critical temperature of the bighorn sheep appears to be below that of most other species of comparable body size. Bianca (1976) found the lower critical temperature of domestic sheep to be -3°C and that for cattle to be about 0°C. Blaxter (1969) cites -3°C and -1°C as the respective critical temperatures of sheep, with 100 mm of fleece on maintenance diet, and cattle, with normal coat depth on full feed showing 500 g daily gain. Webster and Blaxter (1966) reported a mean increase in metabolic rate of Cheviot and Suffolk sheep of 44% between 0° and -10°C, sufficient to indicate a lower critical temperature in this region.

However, Webster et al. (1969, 1970) suggests that metabolic acclimatization occurs in sheep and cattle wintered outdoors, reducing their lower critical temperatures to near -25° and -12°C respectively. It should be noted that this depression is usually accomplished by elevating forage intake to well over maintenance and increasing overall resting metabolic rate during winter. This manner of extension of the thermoneutral range is deceptive; its foundation may be based on an unnatural increased availability of feed in winter to sustain an elevated metabolism. At the time of these trials, the bighorn were on a voluntary below maintenance diet, as was indicated by their weight stasis or loss. The extremely low

critical temperatures which have been reported by several authors for domestic sheep are thus comparable only if the animals were on a maintenance or below maintenance diet prior to the time of measurement.

Holter et al. (1975) found minimum energy expenditure in white-tailed deer at 12°C in winter and an increase in resting metabolic rate of approximately 27% between 0° and -20°C during winter. Fasting metabolism was increased by white-tailed deer between 30 and 50% in mid-winter as controlled temperature was reduced from 0° to approximately -15°C ( Silver et al. 1971). Wesley et al. (1973) suggested the lower critical temperature of the pronghorn antelope was between -13° and -23°C.

The winter thermal comfort zone of the bighorn sheep extends from between -20°C and -30°C to at least 10°C, although panting and behavioral responses on unusually warm days in March indicated the upper end of the range in winter coat to be only a few degrees above 10°C. This suggests that their optimal habitat would be characterized by climatic conditions providing temperatures within this range. Table 4.1 summarizes readings from two weather stations in areas of the Rocky Mountains relatively heavily populated by bighorn sheep, revealing no periods during which average winter temperatures exceed the bounds of the thermoneutral range.

TABLE 4.1

MEAN AMBIENT TEMPERATURE IN THE JASPER AND BANFF AREA 1941 - 1971.
(COURTESY OF ATMOSPHERIC ENVIRONMENT, ENVIRONMENT CANADA).

| JASPER | | | BANFF | | |
|---|---|---|---|---|---|
| TEMPERATURE °C | | MONTH | TEMPERATURE °C | | |
| Minimum | Maximum | MEAN | Minimum | Maximum | MEAN |
| | | January | | | |
| -17.3 | -7.1 | -12.2 | -16.3 | -6.1 | -11.2 |
| | | February | | | |
| -12.7 | -0.4 | -6.6 | -12.9 | -0.7 | -6.8 |
| | | March | | | |
| -8.9 | 3.5 | -2.7 | -10.2 | 2.5 | -3.8 |
| | | April | | | |
| -3.1 | 9.7 | 3.3 | -3.7 | 8.3 | 2.3 |
| | | May | | | |
| 1.4 | 16.0 | 8.7 | 0.7 | 14.2 | 7.5 |
| | | June | | | |
| 5.4 | 19.6 | 12.5 | 4.4 | 17.8 | 11.2 |
| | | July | | | |
| 7.5 | 22.9 | 15.2 | 6.6 | 22.3 | 14.5 |
| | | August | | | |
| 6.6 | 21.5 | 14.1 | 5.7 | 21.0 | 13.4 |
| | | September | | | |
| 2.9 | 16.9 | 9.9 | 2.1 | 16.0 | 9.1 |
| | | October | | | |
| -1.1 | 10.6 | -4.8 | -1.3 | 9.7 | 4.2 |
| | | November | | | |
| -8.4 | 0.8 | -3.8 | -8.3 | 0.7 | -3.8 |
| | | December | | | |
| -13.6 | -0.6 | -9.1 | -13.1 | -4.4 | -8.7 |

It can be argued that these monthly means do not furnish precise enough information to describe the true climate of bighorn habitat. However, it would seem that an average profile of seasonal temperatures would most closely correspond to the basis on which natural selection, or adaptation, to the climatic environment could occur.

Assuming this hypothesis is correct, it is logical that grounds for assessment of successful adaptation should be mean, rather than extreme temperatures, as they are the ones most regularly encountered. To be able to meet all ambient temperatures without increasing metabolic rate above thermoneutral level would be desirable, yet in northern climates this may be physiologically impossible. Survival is definitely favored, however, if average temperatures can be encountered in this manner, as energy conservation has been shown to be at times the most viable strategy available to northern wild ruminants (Moen 1976; Silver et al. 1971).

Many authors have stated categorically that metabolism is not adaptive to ambient temperature. Bartholomew (1968b), Irving et al. (1955), Scholander et al. (1950), and others have suggested that there is no concrete proof of basal metabolic rate modifications due to season or temperature by season effect, and that seasonal differences in metabolic rate and temperature regulation can be explained on the basis of changes in insulation. These statements may accurately depict shorter term responses to cold, for

example on a seasonal or even life-time basis. However, they cannot preclude an evolutionary adaptation to cold occurring over tens of thousands of years. The concept of adaptation to a given environment is accepted and Green (1971) has defined the test of fitness to a given niche as successful occupation of it. There is no reason to suspect that adaptation to a discrete environment would see modification of all life functions except energy metabolism.

Webster (1974, citing Hammel 1964) proposes that acclimatization to cold can occur in several distinct manners, two of which are hypothermic and metabolic acclimatization. The former is characterized by increased insulation and reduced thermogenic response to cold thus fostering energy conservation, while the latter mechanism favors maintenance of homeotherny via high levels of intake reflected in elevated metabolic rate. The elevated thermoneutral metabolic response shown by domestic animals to achieve depression of lower critical temperature most closely associates them with Hammel's latter category, metabolic acclimatization.

Bighorn sheep best fit the description of hypothermic acclimatization. The low critical temperature shown by the animals, without corresponding increase in winter thermoneutral resting metabolism, suggests both high insulation values and reduced peripheral and central sensitivity to cold. In addition, their invocation of closed

standing posture (which can be visualized as an animal standing with all feet on a very small platform) as temperature approached -20°C implies that bighorn sheep use behavioral mechanisms to reduce the temperature at which increased energy expenditure must be initiated to assure survival. Jacobsen (1973), Moen (1973), Stevens (1972) and others report similar findings for other wild ruminants.

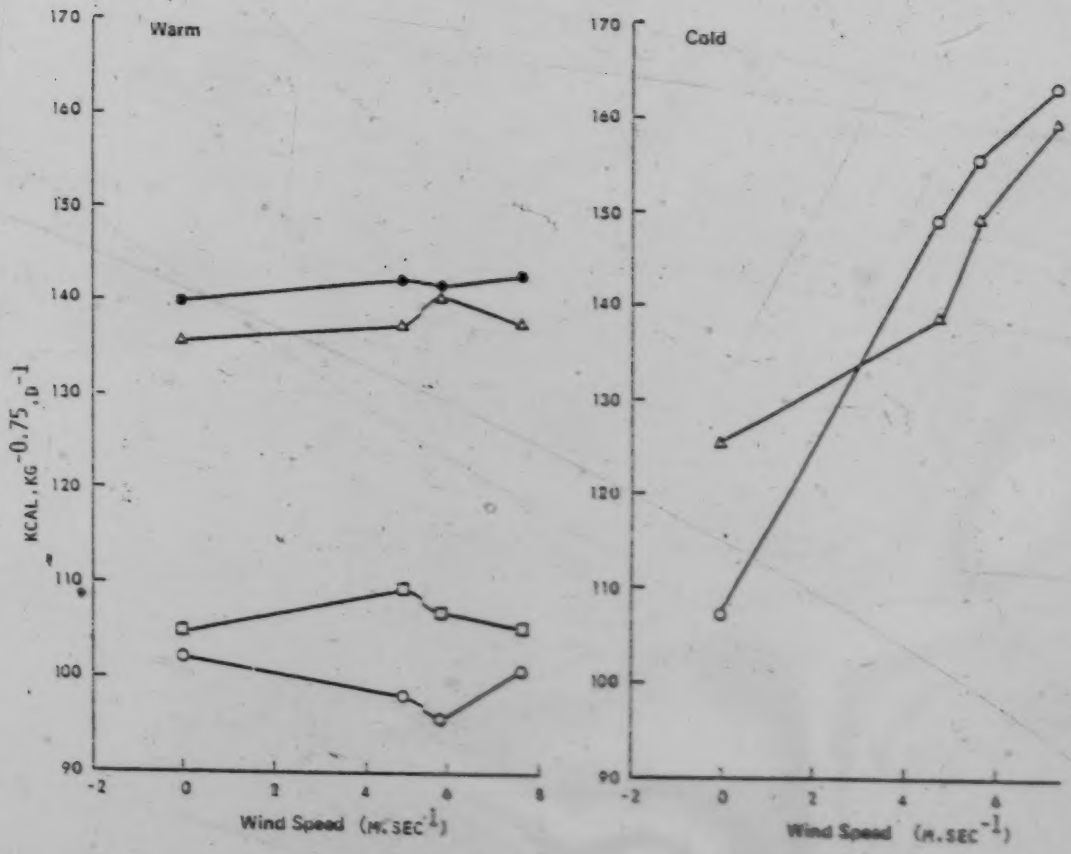
4.2.2. Effect of Wind on Resting Metabolic Rate

The results of six wind tunnel trials, four conducted above -20° and two below are summarized in Fig. 4.2. No significant metabolic response ($P<0.05$) was evoked with wind speeds of 4.9, 5.8, or 7.6 $m.sec^{-1}$ at ambient temperatures above -20°C. Two animals, one ewe and one ram, showed significant ($P<0.05$) increases above resting metabolic rate when air temperatures were -21° to -23°C. Increments in metabolic rate between low and medium wind speed or between medium and high speed were not significant. However, those between no wind and low wind speed (for F2) and between low and high wind speed for both F2 and M1 were significant.

Metabolic rates recorded during the trials at warmer temperatures (-9° to -17°C) were, for the ewes, generally the same as resting metabolic rates at -10°C for late February when the trials were conducted. The rams, however, showed average metabolic rates considerably higher than those for the same period at -10°C. The difference can be

FIG. 4.2 METABOLIC RATE ($KCAL.KG^{-0,75}.D^{-1}$) OF ROCKY MOUNTAIN BIGHORN SHEEP IN RELATION TO WIND SPEED AT ABOVE $-20^{o}C$ (LEFT) AND BELOW $-20^{o}C$ (RIGHT)

(SYMBOLS AS IN FIG. 4.1)


Warm
Cold
KCAL. KG$^{-0.75}$ D$^{-1}$
170
160
150
140
130
120
110
100
90
-2
0
2
4
6
8
Wind Speed (M. SEC$^{-1}$)

explained only on the basis of stress in a new situation, as the animals received only one training period in the wind tunnel prior to test. One animal (M1) on his third time in the tunnel (at -21°C) exhibited a RMR in still air that was within 4 $kcal.kg^{-0.75}.d^{-1}$ of his resting rate in March at -10°C.

The number of trials conducted was insufficient to establish statistically significant trends for changes in insulation. However, as would be expected external insulation declined less at higher temperatures (28.2 ± 4.3 to 21.2 ± 3.5 $°C.Mcal^{-1}.m^{-2}.d^{-1}$, no wind to high speed) than at lower temperatures (39.7±1.7 to 22.8 ± 2.0 $°C.Mcal^{-1}.m^{-2}.d^{-1}$) as did total insulation (33.7±6.0 to 32.2±5.0, warm, no wind to high speed versus 45.0±1.5 to 31.3±3.0, cold, no wind to high speed). Changes in rectal temperature between treatments were significant ($P<0.05$). The animals allowed their body temperature to decline by 0.7±0.1 °C from a mean of 38.7±0.2°C over the entire trial period at temperatures above -20°C, while below -20°C rectal temperature declined 1.55 ± 0.05 °C from an initial mean of 38.8±0.3 °C.

The animals took advantage of the allowance within the stanchion for lateral movement of their hind quarters. Approximately 30° of total adjustment (15° each side of center) was possible and at medium and high wind speeds under both temperature regimes they adjusted their angle to

between 5° and 10°. The advantage of this is unknown, however it may be related to the profile of the wind within the tunnel; it was not completely laminar .

The three animals exposed to temperatures between -14° and -17°C and the two exposed to temperatures below -20°C adopted a closed standing posture. The front legs were set back and the hind legs moved forward as if standing on a surface roughly 40 $cm^2$. The back was hunched and the neck and head lowered. These postural changes were likely an attempt to reduce surface area open to the wind and, as may be the case with the angled orientation, to optimize geometry in relation to both mean wind direction and turbulant flow over the coat thereby reducing wind penetration into the air insulating layer within the coat (Moen 1973). Although the animals were able to lie down, they made no attempt to do so, which differs from the findings of Holter et al. (1975) and Stevens (1972) for white-tailed deer.

At wind speeds of 5.8 and 7.6 $m.sec^{-1}$ the same animals stamped and shifted their weight from side to side possibly to reduce conductive heat loss or to aid circulation. As wind speed increased the animals flattened their hair coat. During high wind speed the only ruffling visible was on the upper part of the white rump patch and this appeared confined to a few softer guard hairs. Again, this served to reduce disruption of the air insulation layer within the

coat and confine the heat losses to conduction through the hair coat and convection from the hair coat surface.

The relative success of these postural and physiological modifications in reducing heat loss is visible in changes in skin and hair coat surface temperature. During warmer exposure F2 did not exhibit extensive postural changes and mean coat surface temperature fell from 2.0±0.5°C to -8.5±0.5°C, at high wind speed which was approximately ambient temperature. Mean skin surface temperature decreased by approximately the same amount from 26.3 ± 2.0 °C providing a skin to air gradient of approximately 25°C. However during exposure to -21°C to -23°C hair coat temperature rapidly dropped from -5.0±1.0°C off scale (-15°C) as the wind tunnel was activated at low speed, to what must be assumed was near ambient temperature. However, skin surface temperature declined only 9 °C from 28.9±2.1°C to 19.9±3.8°C. The hair coat aided by postural modifications thus provided a barrier to a temperature gradient of approximately 40°C. Findings were similar for M1.

Moen (1973) provides an excellent treatment of the effects of wind. Generally, it is assumed that forced convection will destroy the air insulation layer surrounding the hair coat by constant removal of "still" warmed air and disrupt the integrity of the coat, reducing both resistance to conductive heat transfer through the guard and under

hairs themselves and replacing a second warm air layer within the coat with new unwarmed air adjacent to the skin. At some ambient temperature increased heat loss by convection and conduction as a result of wind will impose upon the animal an elevated critical temperature necessitating increased heat production to maintain homeostasis.

Thus, wind in warm air is thought to have little effect upon the animal, whereas wind in cold air results in pronounced increases in metabolism. The temperature values which are described by the terms warm and cold differ by species and appear to be determined by the insulating properties of the hair coat and tissue, and their reflection in still air critical temperature, and the heat loss potential of the animal which is a function of body size (Webster et al. 1970). Studies by Moen (1968), Staines (1976), Stevens (1972) and others have indicated the definition of these temperatures may also be profoundly influenced by the behavioral ingenuity of the animal.

Joyce and Blaxter (1964) found relatively little effect of wind on the metabolic rate of fully fleeced Cheviot, Down, and Scottish Blackface sheep at warm temperatures of 9 to 10°C; a significant increase at temperatures from 5° to -3°C occurred with wind, the highest speed of which was lower than the lowest in this study. Webster et al. (1970) reported a significant increase in the resting metabolic

rates of cattle exposed to wind at a mean temperature of -1.0°C, indicating critical temperature was raised by approximately 10°C from a mean of -11.4°C.

There have been few studies which determine the energetic effect on a live wild ruminant of the interaction of wind and temperature. Thus, there is no basic information with which the results of these few trials can be compared. However, Holter et al. (1975) noted a decrease in metabolic rate of one white-tailed deer as a result of a "slight" wind (which was not quantified) at temperatures between -10° and -20°C, while at 0°C no response was evident. The decrease cited appears to be a result of a change from standing to lying position rather than a physiological response to wind per se. Hart et al. (1961) has recorded increases of 100 to 500% over resting metabolic rate in caribou calves exposed to wind of 5.3 to 6.6 $m.sec^{-1}$ at temperatures of 6° to -5°C.

Responses exhibited by the bighorn sheep in these trials indicated that wind up to 7.6 $m.sec^{-1}$ had negligible effects upon energy expenditures at ambient temperatures above -18°C. However wind speeds as low as 4.9 $m.sec^{-1}$ resulted in substantial increases in metabolic rate effectively raising their critical temperature from near -30° to -21°C. The initial wind speed had the greatest effect on energy expenditure. Moen (1973) stated that lower wind velocities have a proportionately greater effect than high velocities. A greater response was evident for F1 than for

M1 which is probably due to the smaller body size of the ewe (63.0 kg versus 70.0 kg.). Moen (1973) reports that smaller thermal diameters are more rapidly and efficiently linked to forced convection than are large diameters.

Table 4.2 summarizes wind measurement for one of the same stations that provided temperature data in Table 4.1. It is apparent that the wind by temperature interaction does not represent a serious energetic threat to bighorn sheep. However, winter ranges are generally exposed to higher than average wind speeds, which, in combination with above average radiant energy loads on to southern exposures, aid in reducing snow cover from critical winter feed supplies. Thus it is possible that on days with below mean temperature, wind could impose upon bighorn sheep an elevated critical temperature necessitating augmented heat production. However, consideration must be given to the behavioral abilities of the animals in selection of microhabitat to reduce or eliminate effective wind, thereby decreasing convective heat loss and lowering critical temperature.

TABLE 4.2 MEAN DAILY WIND SPEED BY MONTH FOR THE JASPER AREA: 1962-1971

(COURTESY OF ATMOSPHERIC ENVIRONMENT ENVIRONMENT CANADA)

| | WIND SPEED IN $M.sec^{-1}$ AND DIRECTION | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| MONTH | North | NE | EAST | SE | SOUTH | SW | WEST | NW | ALL |
| January | 10.4 | 13.3 | 6.4 | 8.5 | 9.0 | 10.4 | 6.7 | 6.6 | 10.7 |
| February | 6.2 | 10.2 | 5.6 | 9.6 | 9.8 | 10.1 | 7.8 | 9.3 | 9.6 |
| March | 14.6 | 12.3 | 5.0 | 11.7 | 8.3 | 9.8 | 6.4 | 12.2 | 10.1 |
| April | 13.8 | 12.8 | 7.2 | 11.5 | 8.5 | 9.8 | 6.7 | 10.7 | 10.1 |
| May | 11.0 | 10.1 | 6.4 | 10.2 | 7.7 | 9.8 | 8.8 | 8.5 | 9.3 |
| June | 11.2 | 9.8 | 4.5 | 10.1 | 7.2 | 9.9 | 7.2 | 9.1 | 9.1 |
| July | 5.0 | 8.6 | 4.8 | 9.8 | 7.4 | 9.0 | 6.6 | 8.5 | 8.3 |
| August | 6.9 | 9.4 | 5.4 | 9.6 | 7.7 | 9.4 | 6.6 | 8.2 | 8.8 |
| September | 9.4 | 10.1 | 4.0 | 9.8 | 7.5 | 9.1 | 6.6 | 7.8 | 8.8 |
| October | 8.0 | 9.1 | 6.6 | 11.8 | 9.1 | 10.6 | 8.3 | 7.7 | 9.9 |
| November | 6.6 | 12.3 | 5.3 | 10.2 | 9.1 | 10.3 | 8.2 | 4.6 | 9.6 |
| December | 9.9 | 13.9 | 9.6 | 8.6 | 9.4 | 10.7 | 8.2 | 5.8 | 10.4 |

4.2.3. Energy Cost of Eating Long Hay

Metabolic performance during trials which examined the cost of eating is summarized in Table 4.3. Both ewes and rams significantly ($P<0.05$) increased their energy expenditure over fasting metabolic rate during the act of eating. Mean increment in energy expenditure due to eating was not significantly different between sexes, although on the basis of $kcal.kg^{-0.75}.d^{-1}$ and $kcal.hr^{-1}$ differences between sexes were apparent. The average percent increase in metabolic rate as a result of the act of eating was 33.4% for ewes and 31.0% for rams, for a mean of 32.2%. Both fasting and eating expenditures included the energy cost of standing.

The values obtained for the increment due to eating are lower than those disclosed by other authors for domestic sheep. Graham (1964) found an increase of 0.54 $kcal.kg^{-1}.hr^{-1}$ for eating cut, dried hay whereas the bighorn sheep augmented their energy expenditure by 0.43 and 0.46 $kcal.kg^{-1}.hr^{-1}$. (ewes and rams, respectively) while eating alfalfa-brome hay. Webster and Hays (1968) noted an energy increment of 13.8 $cal.kg^{-1}.min^{-1}$ for domestic sheep eating alfalfa-brome hay. The ewes and rams in this experiment increased their metabolic rate by 7.1 and 7.6 $cal.kg^{-1}.min^{-1}$. Blaxter and Joyce (1963) and Webster (1972) indicate increases in metabolic rate of 50 to 60%

TABLE 4.3
ENERGY EXPENDITURES OF ROCKY MOUNTAIN BIGHORN SHEEP PRIOR TO AND DURING EATING LONG ALFALFA-BROME HAY

| | F1 | F2 | EWES | M1 | M2 | RAMS |
|---|---|---|---|---|---|---|
| Pre-fed FMR* (kcal.kg$^{-0.75}$.d$^{-1}$) | 85.2±2.93** | 86.8±0.99 | 86.0±1.42 | 108.5±0.84 | 97.9±0.23 | 103.2±2.40 |
| ENERGY EXPENDED WHILE EATING*** (kcal. kg$^{-0.75}$.d$^{-1}$) | 113.5±0.5 | 116.1±3.6 | 114.8±1.09 | 139.2±0.89 | 131.2±4.5 | 135.2±3.07 |
| INCREMENT FOR EATING: | | | | | | |
| kcal. kg$^{-0.75}$.d$^{-1}$ | 28.3 | 29.3 | 28.8 | 30.7 | 33.3 | 32.0 |
| kcal.hr$^{-1}$ | 25.7 | 27.5 | 26.7 | 30.1 | 37.5 | 33.8 |
| kcal. kg$^{-1}$.hr$^{-1}$ | 0.42 | 0.43 | 0.43 | 0.45 | 0.46 | 0.46 |
| cal.kg$^{-1}$. min$^{-1}$ | 7.0 | 7.2 | 7.1 | 7.5 | 7.6 | 7.6 |
| kcal.kg Dry Matter$^{-1}$ | 39.6 | 41.4 | 40.1 | 36.1 | 45.0 | 40.6 |
| kcal.kg Dry Matter$^{-1}$.kg$^{-1}$ | 0.63 | 0.64 | 0.64 | 0.53 | 0.56 | 0.55 |
| MEAN PERCENT INCREMENT | | | 33.4 | | | 31.0 |

*n=3

**STANDARD ERROR

***n=4

due to eating, whereas in these trials the animals raised metabolic rate by only 32%.

Energy increment associated with eating appears substantially lower for bighorn sheep than for domestic livestock. However, Osuji (1973; frrom Osuji 1974) found an increase of only 7.5 $cal.kg^{-1}.min^{-1}$ for domestic sheep eating fresh pasture grass and Christopherson (1971; from Osuji 1974) recorded augmented expenditures of 0.00 $cal.kg^{-1}.min^{-1}$ when sheep ate chopped alfalfa brome hay. Both findings are similar to those of this study and lower than other values for domestic sheep. It may be that their similarity is a function of the form of the material consumed. Per unit weight less energy is expended in eating fresh grass than hay, but per unit dry weight more energy is expended eating fresh grass. Per unit dry weight a smaller energy increment would be associated with consuming a prepared food such as a concentrate or chopped hay than long hay (Webster 1972, Osuji 1974). On this basis Graham's (1964) increment of 9.0 $cal.kg^{-1}.min^{-1}$ (0.54 $kcal.kg^{-1}.hr^{-1}$) for consumption of long hay would be more similar to the values obtained in this study.

An explanation for the discrepancy between the findings of this study and those of others is not apparent. An assumption might be that the animals did not eat as voraciously as do domestic sheep, yet the measurements were made after 72 hours of fasting. Their mean consumption for

675 and 825 g.hr$^{-1}$ for ewes and rams respectively, which is at the upper end of consumption for domestic sheep as determined by Graham (1964) and Osuji (1974).

The primary purpose for inclusion of this information is to provide additional data which can be used in formulation of a more comprehensive energy budget for bighorn sheep. In field studies often no opportunity exists to weigh an animal or determine exactly the amount of forage it is consuming. Therefore, while the relationship between energy increment and body weight, and also between energy increment and amount consumed, appears to reduce sex differences, the most valuable expression may be the mean base of kcal.hr$^{-1}$. Although more accuracy could be obtained if both sex and weight of a particular animal was known, an estimate of energy increment for time spent eating of 26.7 kcal.hr$^{-1}$ for ewes and 33.8 kcal.hr$^{-1}$ for rams, or even a species mean of 30 kcal.hr$^{-1}$, would satisfy the constraints of a field study.

The cost of grazing would seem to be higher than that for eating hay. However, Graham (1964) determined them to be the same for domestic sheep. Even so, an elevation of the increments noted here must be expected under field conditions of sparse ground cover or reduced access to forage because of snow.

### 4.2.4. Energy Increment of Standing over Lying

Table 4.4 summarizes data on standing and lying resting metabolic rates obtained for two animals. In the first observation perod F1 increased metabolic rate by 13.03 kcal.hr$^{-1}$ (18.3%) associated with a postural change from lying to standing. In the second her increment was 14.3 kcal.hr$^{-1}$ (19.4%) providing a mean increase of 13.67 kcal.hr$^{-1}$ or 18.9%. M1 augmented metabolic rate by 15.5 and 14.96 kcal.hr$^{-1}$ (18.7 and 17.4%) when changing from lying to standing, a mean increment of 15.23 kcal.hr$^{-1}$ or 18.1%.

Many authors have estimated the energy cost of standing over lying for a variety of species (see review of Osuji (1974). Graham (1964) determined the increment for domestic sheep to be 0.34 kcal.kg$^{-1}$.hr$^{-1}$, however his sample was limited to one animal. Other findings for this species have ranged from 0.06 (Osuji, 1973) to 0.38 kcal.kg$^{-1}$.hr$^{-1}$ (Armsby and Fries 1915; from Osuji 1974). Standing increments for cattle have been estimated at levels from 0.06 kcal.kg$^{-1}$.hr$^{-1}$ (Blaxter and Wainman 1962) to 0.12 kcal.kg$^{-1}$.hr$^{-1}$ (Webster pers. comm. to Blaxter 1969). For domestic animals a generally accepted increase in metabolic rate associated with standing as compared to lying is 10% (Blaxter 1969).

TABLE 4.4
RESTING METABOLIC RATE OF ROCKY MOUNTAIN BIGHORN SHEEP WHILE LYING AND STANDING AND ENERGY INCREMENT FOR STANDING

| | F1 | | | M1 | | |
|---|---|---|---|---|---|---|
| | Observation 1 | Observation 2 | Mean | Observation 1 | Observation 2 | Mean |
| RESTING METABOLIC RATE ($kcal.hr^{-1}$) | | | | | | |
| 1. Lying* | 71.04±0.84** | 73.83±1.76 | 72.44 | 82.93±0.98 | 85.93±77 | 84.35 |
| 2. Standing* | 84.07±0.77 | 98.13±1.24 | 86.1 | 98.43±0.81 | 100.73±1.59 | 99.58 |
| ENERGY INCREMENT For Standing | | | | | | |
| $kcal.hr^{-1}$ | 13.03 | 14.3 | 13.67 | 15.5 | 14.96 | 15.23 |
| $kcal.kg^{-1}.hr^{-1}$ | 0.21 | 0.23 | 0.22 | 0.24 | 0.22 | 0.23 |
| $kcal.kg^{-0.75}.hr^{-1}$ | 0.59 | 0.65 | 0.62 | 0.68 | 0.66 | 0.67 |
| Percent | 18.3 | 19.4 | 18.9 | 18.7 | 17.4 | 18.1 |

*N=3
**STANDARD ERROR

The energy cost of standing has been examined for several species of wild ruminants with considerably less consensus. Wesley et al. (1973) found that an additional 1.9 $kcal.kg^{-0.75}.hr^{-1}$ was needed for pronghorn antelope to maintain standing posture over lying. Roe deer exhibited an energy increment of 1.1 $kcal.kg^{-0.75}.hr^{-1}$ or 22% when standing as compared to lying (Weiner 1977). Mattfeld (1973) suggested an increase of 0.23 $kcal.kg^{-0.75}.min^{-1}$ or 13.2 $kcal.kg^{-0.75}.hr^{-1}$ is necessary to maintain standing as compared to lying posture for white-tailed deer. Given the findings of other authors this factor seems unreasonably high. Gates and Hudson (in review) found that Rocky Mountain wapiti spend an additional 0.24 $kcal.kg^{-1}.hr^{-1}$ when standing, producing an increment in energy expenditure of 18.6% over lying resting metabolic rate. The magnitude of difference evident in findings for wild animals suggest either lack of standardization of technique (for example, utilizing measurements of stressed animals) or profound dissimilarities in skeletal and muscular structure.

It appears that the increments noted for the cost of standing in bighorn sheep are higher than those for domestic animals and generally lower than those for other wild ruminants, with the exception of values obtained for wapiti. A reason for the former difference may be related to anatomical differences between bighorn sheep and domestic animals. The angle created by the spinal column and hind leg in a horse is virtually 90° when the animal is standing

relaxed, as is the angle between the ground and the hind leg and the back is more or less parallel to the ground. This apparently allows the horse to bear part of its weight efficiently with a negligible energy cost for standing over lying (Blaxter, 1969). Other domestic animals exhibit angles that diverge from 90° and show some energy cost associated with standing.

Examination of the skeletal structure of a bighorn sheep reveals an angle considerably greater than 90° between the spinal column and the hind leg, and the ground and hind leg form an angle much less than 90°. In addition, the back is not parallel with the ground, as the hind quarters are elevated above the shoulders. These differences would appear to be an adaptation to movement on steep terrain, particularly upward. However, on flat ground additional muscular work is necessitated to prevent the hind legs from buckling and to support the weight of the hind quarters, abdominal section and part of the chest. Visualization of this may be difficult. However, examination of the standing posture of bighorn sheep reveals that they never appear to be relaxed; their standing posture is analogous to a loaded spring, always on the edge of release. It is possible that the higher cost of standing in comparison to domestic animals is a function of muscular tension resulting from bone structure and carriage differences.

# 5. AN EXPLANATORY MODEL

## 5.1 Introduction

Documentation of important components of the bioenergetic life history of an animal provides a basis to which all activities can be related and enables quantitative measure of ecological success. Researchers in both behavioral (Geist 1971; Moen 1973; Shackleton 1973; Staines 1976) and physiological fields (Holter et al. 1975; Silver et al. 1969; Stevens 1972; Weiner 1977) have adopted this approach.

Various workers have attempted to discover the base to which differences in species, sex, age, nutrition, and environmental parameters could be normalized mathematically. The most generally acceptable equation is accredited to Benedict (1938) or Kleiber (1947) wherein basal metabolic rate (BMR) is expressed by:

$$B.M.R.\ (kcal.kg^{-1}/.) = 70 * W(kg)^{0.75}$$

Because of its generality the functional value of such an equation is limited. Other research has endeavored to establish models which explain the metabolic rate of a particular species by inclusion of parameters of significance. Graham et al. (1974) developed an equation to predict BMR (M; Kilojoules.$d^{-1}$) in domestic sheep on the basis of metabolic body weight (W), age in years (A), prior

weight gain (G; $g.d^{-1}$), and pre-fasting intake of digestible energy (D; $Megajoules.d^{-1}$):

$$M = 257\ W * e^{-0.083A} + 2.8G + 46\ D$$

Utilizing results of telemetrically-measured heart rate, Holter et al. (1976) designed the following predictive equation for white-tailed deer:

$$M = 33 + \begin{cases} \text{Summer} & 17 \\ \text{Fall} & 11 + 1.89\ HR - 0.142\ AMBT - 0.012\ AMBT^2 \\ \text{Winter} & -29 \\ \text{Spring,} & 0 \end{cases}$$

where M is metabolic rate in $kcal.kg^{-0.75}$., HR is heart rate in beats $min^{-1}$, and AMBT is ambient temperature in degrees C.

In this study, the prescient model was used to determine if variation in the energetics of Rocky Mountain bighorn sheep could be explained by application of factors from measurable changes in physical, nutritional, and environmental variables applied to a basic or average metabolic rate.

## 5.2 RESULTS AND DISCUSSION

### 5.2.1. Selection of Predictor Variables

Simple correlation analysis revealed associations between several independent variables and metabolic rate which were further examined using Multiple Classification

Analysis. Elimination of predictors and predictor associations was done as outlined in Methods. In addition, some attention was paid to the practicality of providing appropriate information. For example, although mean of global solar radiation two weeks prior accounted for 45% of the variation in metabolic rate, it was felt that the difficulty in collecting such data outweighed its usefulness as a predictor.

The best model included sex, date, nutritional status, exposure temperature (°C), body weight (kg), mean ambient temperature three days prior to trial (°C), and mean gross energy intake ($kcal.kg^{-0.75}$.) two weeks prior to trial.

5.2.2. Predictor Variable Statistics

Eta$^2$ coefficients for the seven predictors ranged from 0.02 to 0.40. Corresponding Beta values ranged from 0.17 to 0.52. The simple correlation had little influence upon the strength of the predictor when adjustment was made for effects of other members of a predictor group. Date and trial (exposure) temperature were consistently the strongest predictors[1] on the basis of Beta values yet their Eta$^2$ values were among the lowest.

5.2.3 Predictor Coefficient Profiles

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[1] This finding is in accord with that of Holter et al. (1975) for white tail deer.

The primary advantage of MCA was its ability to handle categorical predictor variables; for each category of each predictor a coefficient was expressed as a deviation from the grand mean. Formulation of predictor categories was made on the basis of important distinctions within the scope of the variable.

Interpretation of a multiple classification analysis thus centers on examination of the category adjusted coefficients. The latter are summarized in Table 5.1. The patterns exhibited by coefficients are largely self-evident. Males showed at all times a higher metabolic rate than females (Fig. 5.1). Energy expenditure varied seasonally, being lowest in winter and highest in late spring, although this variation was likely heavily influenced by the effects of other variables (Fig. 5.2). By predictor elimination it was found that weight had the most profound effect upon season coefficient patterns, altering them from a linear change from fall to spring to the more quadratic form exhibited in Fig. 5.2.

After fasting for 72 hours, animals exhibited lower energy expenditures than when feeding ad libitum (Fig. 5.3). Elimination procedures indicated that the poor predictive value of nutritional status was due to partition between its effect and that of the level of gross energy intake predictor. Nutritional status also shaped the coefficient patterns shown by trial or exposure temperature (Fig. 5.4).

Table 5.1 Statistical Evaluation of Factors Influencing Over-winter Energy Expenditure of Rocky Mountain bighorn sheep

| Predictor Variable and Categories | $Eta^2$ | Category Coefficients * ($Kcal.d.^{-1}$) | Beta |
|---|---|---|---|
| Sex | 0.3137 | | 0.1969 |
| 1 Female | | -117.45 | |
| 2 Male | | 117.45 | |
| Date | 0.1674 | | 0.5255 |
| 1 Aug.-Oct. | | -93.23 | |
| 2 Nov.-Feb. | | -250.43 | |
| 3 Mar.-Apr. | | 240.10 | |
| 4 May-June | | 864.13 | |
| Nutritional Status | 0.0912 | | 0.1738 |
| 1 Fed | | 45.45 | |
| 2 Fasted | | -237.37 | |
| Trial Temperature ($^{o}C$) | 0.2799 | | 0.4524 |
| 1 -35 to -20 | | 1470.00 | |
| 2 -20 to -10 | | -28.90 | |
| 3 -10 to 0 | | -28.24 | |
| 4 0 to 10 | | -90.14 | |
| Body Weight (Kg.) | 0.4022 | | 0.3564 |
| 1 50.0 to 62.0 | | -285.91 | |
| 2 62.1 to 65.0 | | -122.60 | |
| 3 65.1 to 70.0 | | 31.74 | |
| 4 70.1 to 75.0 | | 87.88 | |
| 5 75.1 to 80.0 | | 361.44 | |
| 6 80.1 to 88.0 | | 322.41 | |
| Ambient Temperature ($^{o}C$) | 0.0246 | | 0.2322 |
| 1 -35 to -10 | | 45.38 | |
| 2 -10 to 10 | | 56.59 | |
| 3 10 to 35 | | -359.57 | |
| Gross Energy Intake per $Kg.^{0.75}$ | 0.0406 | | 0.2676 |
| 1 3.6 to 162.0 | | -128.78 | |
| 2 162.2 to 183.9 | | -210.24 | |
| 3 184.0 to 216.0 | | -53.62 | |
| 4 216.1 to 275.9 | | 202.10 | |
| 5 276.0 to 430.0 | | 223.64 | |

* Grand Mean for Model: 2631.87 $Kcal.d.^{-1}$

FIG. 5.1 LEAST SQUARES MEANS OF METABOLIC RATE OF ROCKY MOUNTAIN BIGHORN SHEEP EWES AND RAMS

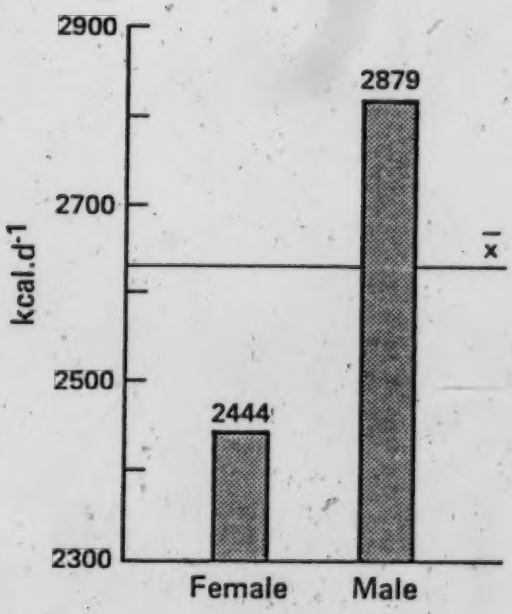

2900
2700
2500
2300
kcal.d-1
2879
2444
x̄
Female
Male

FIG. 5.2 LEAST SQUARES MEANS OF METABOLIC RATE OF ROCKY MOUNTAIN BIGHORN SHEEP IN RELATION TO DATES OF MEASUREMENT

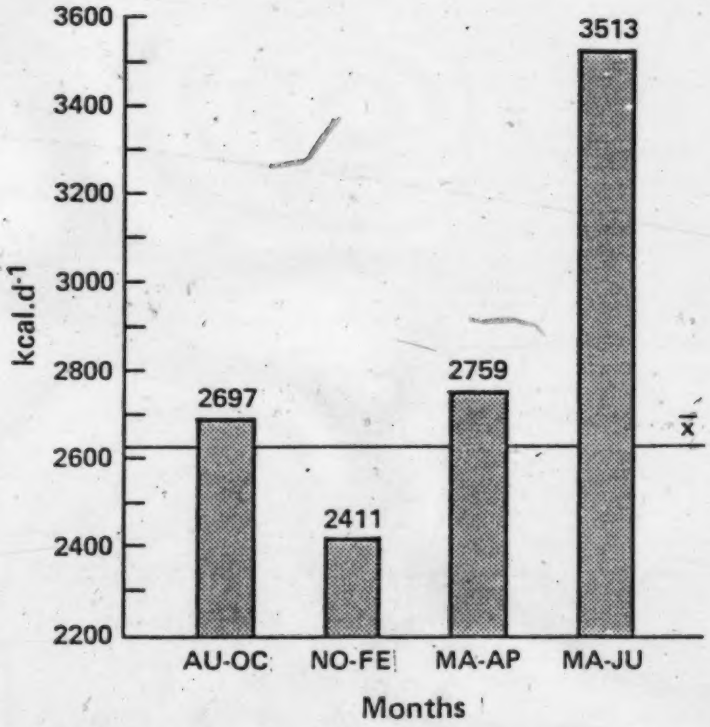

3600
3400
3200
3000
2800
2600
2400
2200
kcal.d-1
2697
2411
2759
3513
x̄
AU-OC
NO-FE
MA-AP
MA-JU
Months

FIG. 5.3 LEAST SQUARES MEANS OF METABOLIC RATE OF ROCKY MOUNTAIN BIGHORN SHEEP FED OR FASTED 72 HOURS

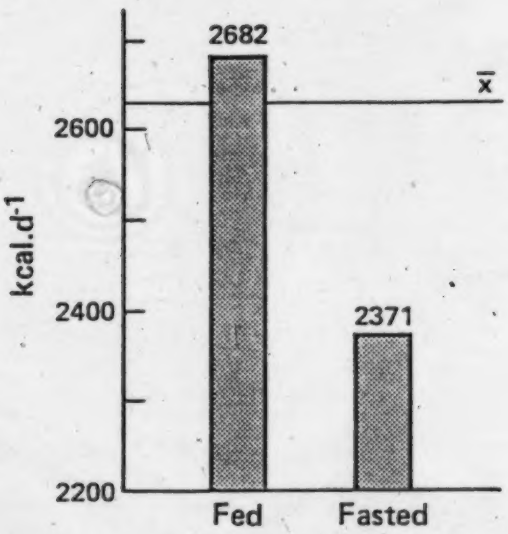
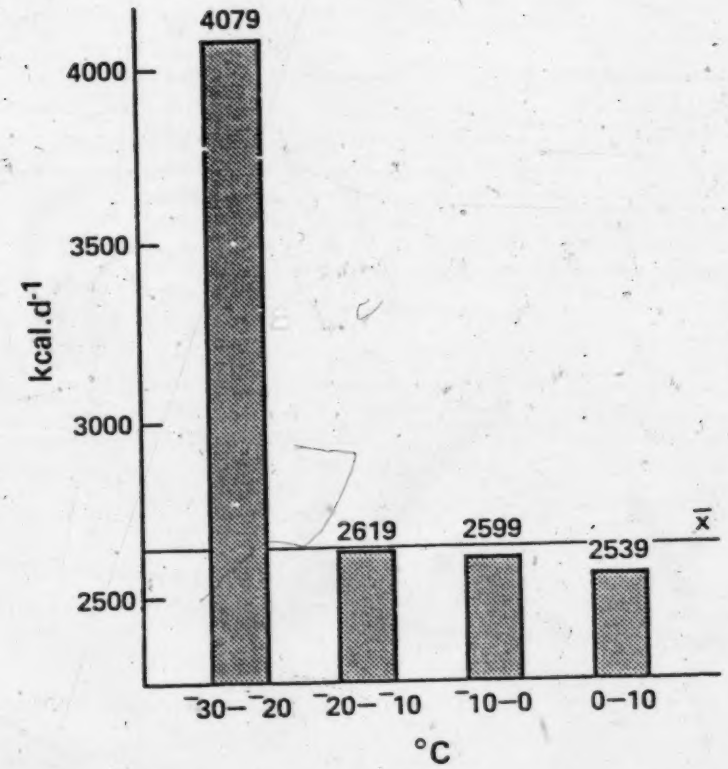

2682
$\bar{x}$
2600
kcal.d$^{-1}$
2400
2371
2200
Fed
Fasted

FIG. 5.4 LEAST SQUARES MEANS OF METABOLIC RATE OF ROCKY MOUNTAIN BIGHORN SHEEP IN RELATION TO EXPOSURE TEMPERATURE


4079
4000
3500
3000
2500
kcal.d-1
2619
2599
2539
x̄
⁻30—⁻20
⁻20—⁻10
⁻10—0
0—10
°C

The adjusted means for categories below -10°C were in general agreement with findings of another section of this study which showed an obvious lower critical temperature in the region of -20°C to -30°C. However, the coefficients indicated a continual, although minor, decline in metabolic rate as temperature increased from -20° to -10°C, whereas metabolic rate actually increased at temperatures above -10°C. Elimination of nutritional status from the model resulted in the correct pattern, suggesting that the analysis may have unnaturally partitioned the effect of temperature and nutritional influence on energy expenditure due to the high correlation between predictor categories.

Metabolic rate was almost linearly related to body weight (Fig. 5.5). The small change between the upper two categories perhaps could be explained by the significant contribution made to the highest category by the largest male, who was particularly relaxed in the experimental situation. Fig. 5.6 suggests that prolonged exposure to low temperature may result in an adaptive response, in contrast to the acute sensitivity exhibited in Fig. 5.4. The categories of ambient temperature also were strongly intercorrelated with those of date.

Gross energy intake (Fig. 5.7) adjusted means have been corrected for body weight, but are intercorrelated with sex and season. Contribution to the lowest category was made by animals in rut and in early spring when intake fell off but

FIG. 5.5 LEAST SQUARES MEANS OF METABOLIC RATE OF ROCKY MOUNTAIN BIGHORN SHEEP IN RELATION TO BODY WEIGHT

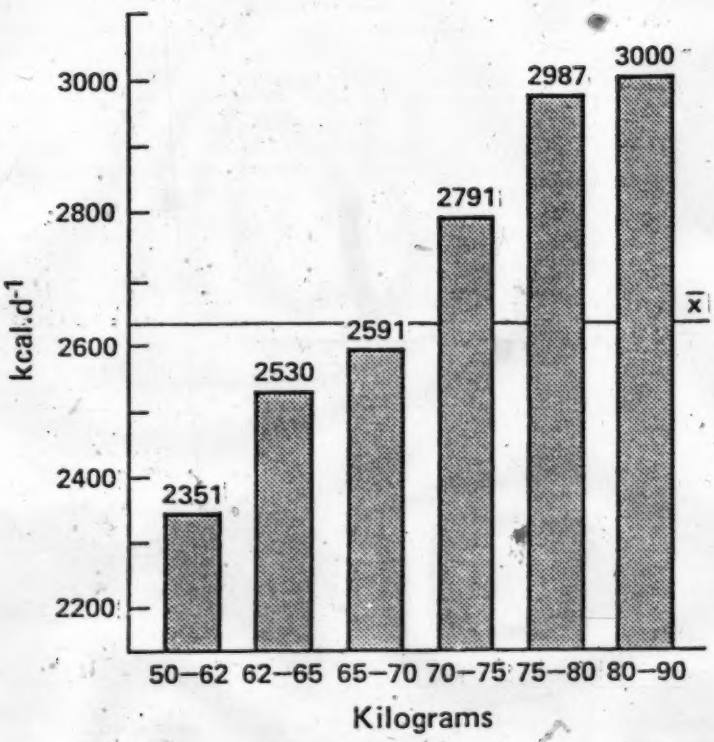

3000
2800
2600
2400
2200
kcal.d-1
2351
2530
2591
2791
2987
3000
x̄
50–62
62–65
65–70
70–75
75–80
80–90
Kilograms

FIG. 5.6 LEAST SQUARES MEANS OF METABOLIC RATE OF ROCKY MOUNTAIN BIGHORN SHEEP IN RELATION TO MEAN AMBIENT TEMPERATURE THREE DAYS PRIOR

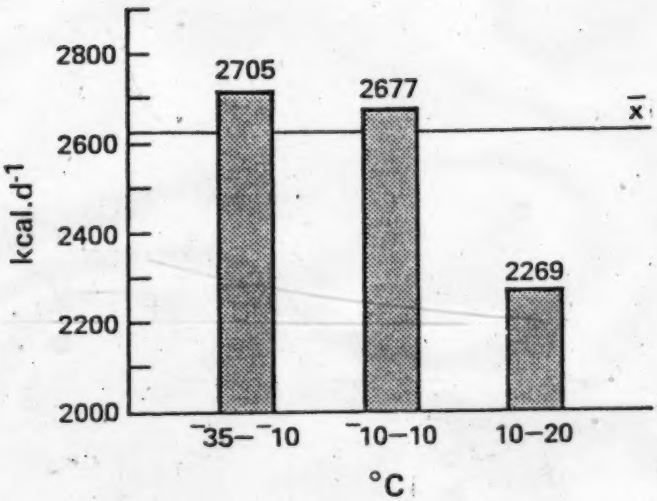
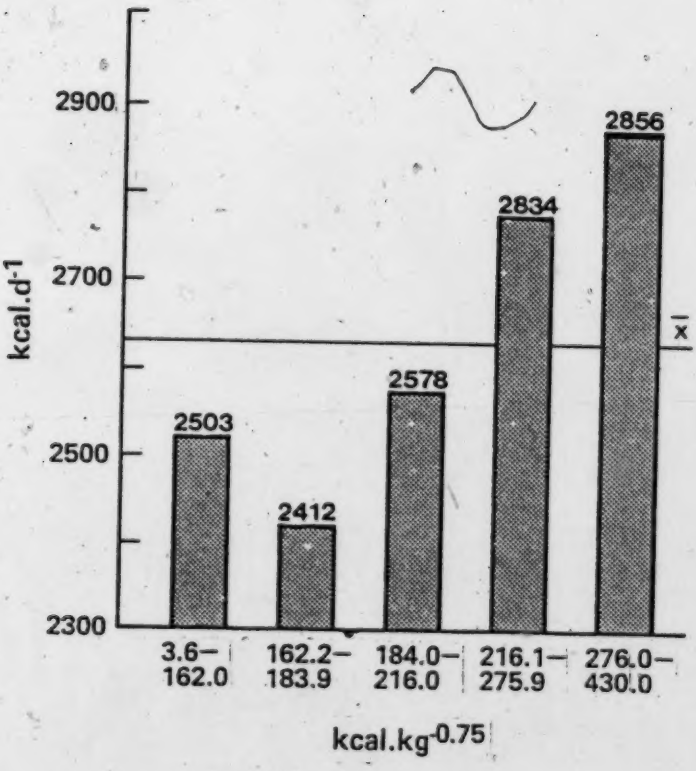

2800
2600
2400
2200
2000
kcal.d-1
2705
2677
2269
x̄
⁻35—⁻10
⁻10—10
10—20
°C

FIG. 5.7 LEAST SQUARES MEANS OF METABOLIC RATE OF ROCKY MOUNTAIN BIGHORN SHEEP IN RELATION TO MEAN GROSS ENERGY INTAKE TWO WEEKS PRIOR


2900
2700
2500
2300
kcal.d-1
2503
2412
2578
2834
2856
x̄
3.6–
162.0
162.2–
183.9
184.0–
216.0
216.1–
275.9
276.0–
430.0
kcal.kg-0.75

energy expenditure was elevated. Otherwise the effect of increased intake on metabolic rate was almost linear.

5.2.4 Performance and Operation of the Model

The model as used in the context of this paper was explanatory rather than predictive. Table 5.2 summarizes the $R^2$ unadjusted and adjusted values and significance tests for the model presented. The model was highly significant both on the basis of unadjusted and adjusted multiple correlation coefficients ($P<0.01$) and the calculated F value ($P<0.005$).

In order to use the model in a predictive manner the user must describe the animal in terms of the predictors and their categories, select the appropriate coefficients, and add them to the grand mean to obtain a figure of metabolic rate in kcal.$d^{-1}$ for that individual. To determine the energy expenditure of a bighorn ewe in April who had been feeding at a level of 3500 kcal. per day, whose weight was approximately 66 kilograms, on a day when the exposure temperature for the three previous days was 3.7°C, the following coefficients would be selected from Table 5.1:

| | | |
|---|---|---|
| sex: | -117.45 | (female) |
| date: | +240.1 | (November-February) |
| nutritional status: | 45.45 | (fed) |
| trial temperature: | -90.14 | (0° to 10°C) |
| body weight: | 31.74 | (65 to 70 kilograms) |
| Ambient temperature: | 56.59 | (-10° to 10°C) |

Table 5.2 Statistical Evaluation of a Predictive Model of Over-winter Energy Expenditure of Rocky Mountain bighorn sheep

| | |
|---|---|
| $R^2$ unadjusted obtained | 0.8697 |
| $R^2$ adjusted obtained | 0.8459 |
| $R^2$ (0.01) necessary for significance | 0.0645 |
| F value calculated | 36.53 |
| F (0.005, d.f.) necessary for significance | 2.19 |
| Model Degrees of Freedom | 19 |

G.E. Intake: -128.78 (3.6 to 162 kcal.kg$^{-0.75}$) and add them to the grand mean of 2631.87 in Y = 2631.87 + (-117.45) + 240.1 + 45.45 + (-90.14) + 31.74 + 56.59 + (-128.38) = 2669.38. The predicted value for that animal is then 2669 kcal.d$^{-1}$ or approximately 2670 kcal.d$^{-1}$ (actual measured metabolic rate was 2691 kcal.d$^{-1}$).

The model presented in this paper was not developed, and has not been tested, for its prediction capabilities. The standard method for achieving a verification of the prescient accuracy of a given model is to hold back a data block from use in the design phase and call upon the model to predict scores for the dependent variable on the basis of input predictor descriptions. As all of the data from this study was used in construction of the model such confirmation was not possible. However, the $R^2$ adjusted coefficients, which have been corrected for capitalizing on chance in fitting a given model, indicate that a fair degree of confidence could be placed on operation of the models as predictors of metabolic rate for the population from which the bighorn study group was drawn.

If used in such a manner it should be remembered that the scores obtained reflect only resting metabolic rate in kcal.d$^{-1}$ and do not include the additional costs of various normal activities such as walking, running, and feeding. Values of 34 and 27 kcal.hr$^{-1}$ for males and females respectively have been found for the cost of eating cut long

hay (Section 4.2.3). Measurements of costs of walking and running under a variety of terrain types and snow depths for species ranging from domestic sheep to caribou are available in Moen (1973) and Blaxter (1969). Addition of these scalars to the models would allow construction of a daily energy budget, which in turn could serve as a basis to judge the importance of factors creating deviation from the normal behavioral-bioenergetic pattern exhibited by bighorn.

Precursors of the model presented show that a smaller, but nevertheless significant amount of explanation could be obtained when consideration was given only to date, trial or exposure temperature, and body weight or to sex, date, trial temperature and nutritional status. These models and the results of trial elimination, point to the tremendous importance of exposure temperature in determining metabolic rate. Elimination of trial temperature from a predictor set resulted in a minimum reduction in explanatory power of 20%.

The ability of other predictors to influence the shape of seasonal effect on energy expenditure has been mentioned. The research of Silver and associates of the New Hampshire group, and colleagues and students of Moen from Cornell, as well as that of many others who have examined the bioenergetics of wild ruminants points to the existence of seasonal cycles in basic life functions in certain of our indigenous species. The hypothesis has been made that an annual variation in metabolism triggered by external

zeitgeibers such as photoperiod, functions independently of, but colinearily with, climatic and ecological factors such as temperature and available food. The assumption is that lowered metabolism and decreased sensitivity to cold is adaptive in times of food shortage and hostile climate.

The importance of the date variable indicates that a cycle, influenced by seasonal factors other than only temperature, is evident in the energetics of the Rocky Mountain bighorn sheep. Removal of the variable from the model results in a reduction in explanatory power of 12% which suggests that, although significant, the effect of date is less than that of temperature. The existence of an innate cycle was thus indicated in this section of the study. Deviation from an annual mean resting metabolic rate could be explained at a significant level by changes in date, temperature, body weight and nutritional factors.

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# 7. APPENDIX

## Appendix 1

## Treatment of Disease and Parasites

The primary disease problems were related to the Pasteurella - pneumonia syndrome which at times plagued all animals. Clinical signs of the imminent onset of a "bout" were spasmodic coughing, a heavy purulent discharge from the nose, elevated rectal temperature, loss of appetite, dullness of the eyes, and listlessness ( Siegmund 1973 ). Prediction of the onset proved to be the most effective tool. Nasal swabs were taken on a regular basis and sent to the Microbiology Section of the Veterinary Services Division, Alberta Agriculture, for identification and sensitivity testing. Visual cues as mentioned were responded to with rapidity, and rectal temperatures were taken whenever feasible.

In the event of an onset, early treatment produced speedy elimination of symptoms. A variety of antibiotics, both bacteriostatic and bactericidal, were used alone or in acceptable combinations, always at a minimum of twice the recommended dosage. Drugs used were : penicillin (dihydrostreptomycin ), penicillin-L, oxycillin, ampicillin, and tetracycline, administered intramuscularly: triple sulfa, and chloramphenicol, aministered intravenously. Combinations given were: oxycillin I.M. - triple sulfa I.V. and tetracycline I.M. - chloramphenicol I.V..

Tetracycline I.M. produced the most acceptable results;

with the exception of localized irritation (which was later eliminated as a result of using a low irritation water base variety ) minimal stress was created during these treatments. It was felt that the stress associated with the high degree of restraint necessary and the numbers of people involved in an I.V. injection outweighed the advantage of immediate attainment of therapeutic levels.

In the long run, minimization of stress produced the desireable effect of eliminating the occurence of the syndrome; the Pasteurella complex is known to be precipitated by physical or psychological stress ( Siegmund 1973 ). The sheep carried loads of the bacteria ranging from low to heavy throughout the course of the study, but no serious onset of the pneumonic depression was encountered after November, 1975.

Gastrointestinal problems were minimal, limited to the occurrence of small stomach roundworms of the genera Trichostrongylus, Ostertagia, Cooperia, Oesophagostomum, and Haemonchus. Oral drencing was carried out with the antiheminthics thiabendazole, given twice two weeks apart in summer, and levamisol, administered the same way in the late fall.

Coccidial infection was a constant irritation. Oral treatment with the sulfonamide sodium sulfamethazine produced temporary reductions in Eimeria populations, but did not eliminate them completely. In conjunction with the

fall antihelminthic treatment, amprolium was administered orally; follow-up fecal analysis has shown no evidence of either coccidial infection or roundworm infestation.

The bighorns have never shown fecal output of larvae of the lungworm Protostrongylus stilesi or P. rushi, commonly found in free-ranging sheep and associated with the pneumonia complex.